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Larval development of British prawns and shrimps (Crustacea : Decapoda : Natantia)
1 Laboratory methods and a review of *Palaemon* (*Paleander*) *elegans* Rathke 1837

A. A. Fincham

British Museum (Natural History)
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Larval development of British prawns and shrimps (Crustacea : Decapoda : Natantia). 1. Laboratory methods and a review of *Palaemon* (*Paleander*) *elegans* Rathke 1837

BRITISH MUS. NAT. HIST. 29 JUN 1977 PRESENTED ZOOLOGY LIBRARY

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Synopsis

Nine larval and the first post-larval stages of *Palaemon* (*Paleander*) *elegans* are described from specimens reared in the laboratory. The results are compared with data of previous authors concerning larvae and post-larvae from different parts of the known geographical range of the species, both for larvae reared in the laboratory and material from plankton samples. The number of larval moults (6–9) is influenced by environmental conditions, especially temperature.

Introduction

Larval stages of British decapods are poorly known and in 1974 a programme was started in the British Museum (Natural History) to study larval taxonomy of British prawns and shrimps (sub-order Natantia). The overall strategy of this series of papers is:

1. To provide detailed descriptions of all larval stages both for the purposes of identification and as the basis for a future systematic study involving the use of numerical methods.
2. To study morphogenesis and reproductive patterns, especially the variability of structure and differing numbers of larval stages.
3. To review previous work and correlate this with the results of the present research programme.

It is appropriate in such a study to bear in mind the caveat of Gurney (1924): 'A certain amount of caution is necessary in accepting a series of stages as determined under artificial conditions as normal. I have found myself in the case of *Palaemonetes varians* that abnormal intermediate stages may be obtained in captivity . . . .'

Materials and methods

Circulation system for adult-holding bank

Ovigerous *Palaemon* (*Paleander*) *elegans* were collected by handnetting from mid- and low-shore rock pools at Rottingdean, Sussex, England (grid reference: TQ 373019). The species was easy to obtain and served both to test the rearing equipment and to complete the description of larval stages from British waters ably begun by Gurney (1924), but unfinished. Adult prawns were kept in 'Plymouth' sea water (supplied by the Plymouth Marine Laboratory) in a closed circulation system housed in a controlled temperature room at $15 \pm 0{\cdot}5$ °C. A light régime from 0600 to 1730 h was provided by two 1·46 m daylight fluorescent tubes situated 1·5 m from the holding tanks. The animals, which were fed every 2–3 days with dried small crustaceans ('Hykro Shrimp Snack'), survived for several months in the holding bank.

The circulation system (Fig. 1) maintained a supply of clean, filtered sea water. Water from the header tank (Fig. 1a) ($45 \times 45 \times 45$ cm), holding approximately 70 l, gravity feeds through an isolation valve (Fig. 1b) to a distribution pipe (Fig. 1c) which gives equal water pressure to six clear plastic containers with lids (Fig. 1d) ($9 \times 15 \times 27$ cm) in which berried females are held.

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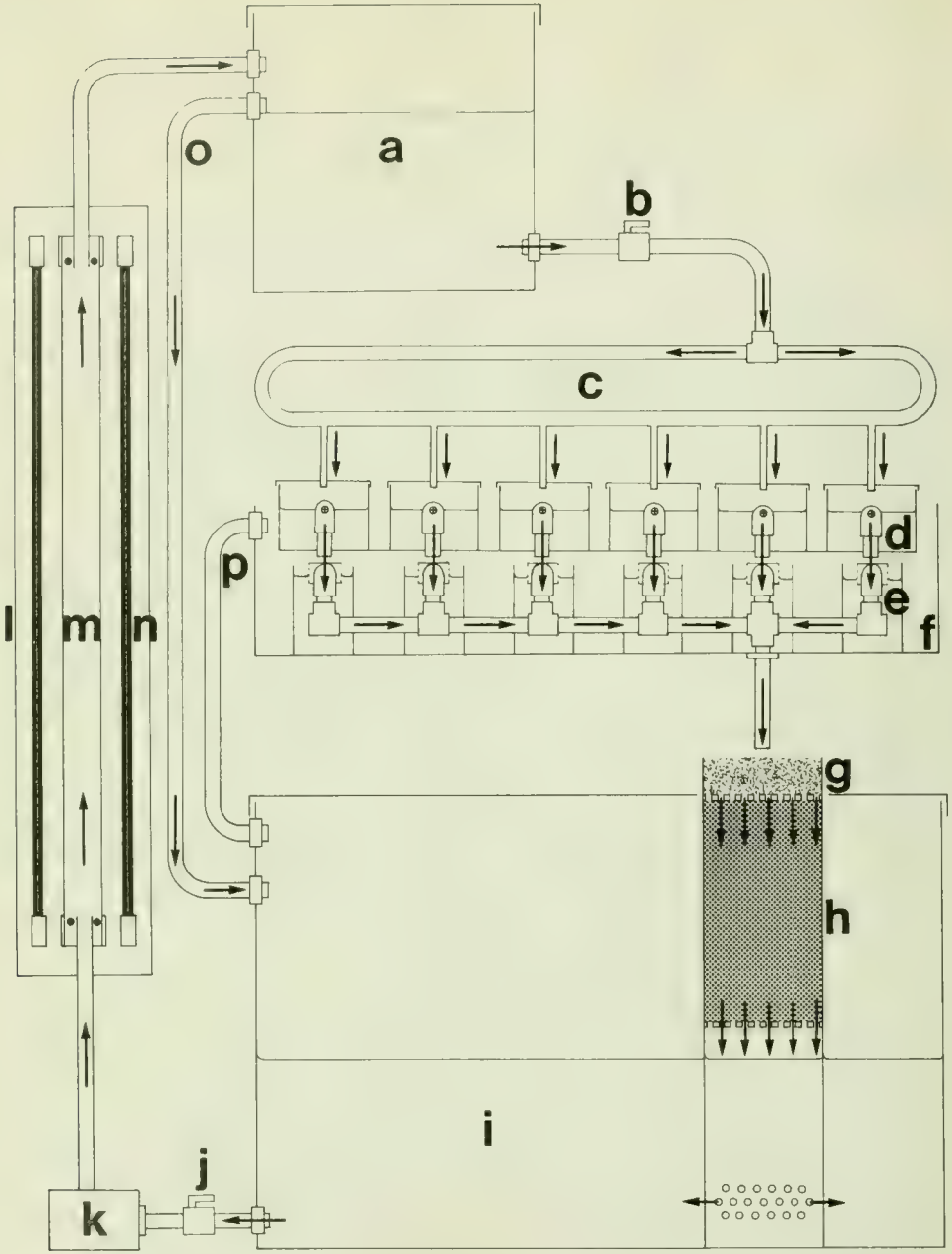

Fig. 1 Sea water circulation system: (a) header tank; (b) valve; (c) ring main; (d) adult-holding containers; (e) larval trap; (f) shallow tray; (g) synthetic fibre filter; (h) biological filter; (i) reservoir; (j) valve; (k) pump; (l) outer alloy case of ultra-violet filter; (m) quartz tubing; (n) ultra-violet tubes; (o, p) overflow pipes. Arrows show direction of water flow.

These containers are supplied with sea water at a rate of 30–35 l/h (providing a complete water change every 6 minutes). The outlet from these containers is guarded with a coarse plastic mesh to prevent the escape of the adult. The larvae, which hatch mainly at night, are collected by a larval trap (Fig. 1e) which separates the adults from larvae and thus reduces cannibalism. The trap consists of a Durapipe 'T' piece, with the ends covered with 0·5 mm nylon mesh, fixed into the side of a 800 ml cylindrical plastic container. These containers, holding a hatch from the previous night, can be lifted from the system and larvae then transferred to either individual or mass culture containers. The adult-holding tanks and larval traps are all placed in a shallow tray (Fig. 1f) which collects spillages and drains into the filter system beneath. The main return from the larval traps is piped direct to the filter to minimize evaporation.

The filter consists of a synthetic fibre (Fig. 1g) to remove any detritus in the circulating water; this part of the filter is replaced every week. The sea water then passes through a biological filter comprising a plastic cylinder (38 cm high × 18 cm diameter) filled with crushed mussel shell. Bacteria in this filter remove complex organic molecules produced by the animals in the system. Samples of water from the top and bottom of the filtering column tested for ammonia, nitrite and nitrate content show that complete nitrification is occurring. Before prawns are placed in the holding tanks, the circulation system is run for 4 weeks at 15 °C in order to build up the bacterial population on the surface of the shell material in the filter. After passing through this biological filter the sea water is collected in a large reservoir (Fig. 1i) (50 × 55 × 90 cm) capable of holding all the water in the system should the pump fail. A valve (Fig. 1j) isolates the pump from the main reservoir so that bearing maintenance can be carried out at regular intervals, usually every 12 months. A Totton Electrical Sales Ltd pump (Model 175B/M/DP) with a ceramic impeller delivers water at 720 l/h to the header tank through a specially designed ultra-violet (UV) filter which helps to limit the build-up of bacteria and fungi in the system. The UV unit consists of a light alloy hexagonal outer case, diameter 20 cm (Fig. 1l) surrounding a 1 m length of quartz tubing (Fig. 1m) of 4 cm internal diameter (ID) which connects by 'O' ring adaptors to the 2 cm ID Durapipe at each end. Fixed inside the casing are six Phillips 90 cm UV tubes (Fig. 1n) at a distance of 4 cm from the quartz tube.

Overflow from the header tank passes through two pipes (Fig. 1o) and is splashed into the reservoir to give effective aeration. A further emergency overflow (Fig. 1p) connects through the trough 'f' to the reservoir. The entire circulation system contains 220 l of sea water, of which 25 l are replaced every 14 days.

'Water quality' (specific gravity, salinity, pH and water temperature) was monitored every 2–3 days from October 1974 to October 1975. Once the system had stabilized after an initial 4 week run-in period these factors remained relatively stable: S.G. 1·026, standard deviation (s.d.) 0·002; salinity 40·1, s.d. 2·7‰; pH 8·07, s.d. 0·18; temperature 17·1, s.d. 0·9 °C. The Electronic Switchgear salinometer was checked as part of an experiment run by the International Council for the Exploration of the Sea (I.C.E.S.) and our readings of 7·976‰ (low salinity Baltic sample) and 38·123‰ (Mediterranean sample) were acceptably close to the means of 8·011‰ and 38·125‰ respectively.

Larval culture

Two methods of culture were used, mass and individual, and in both water and food were changed every 2–3 days. In mass cultures up to 100 larvae were placed in plastic jars containing 1·5 l of Plymouth sea water and 0·02 mg/ml Streptomycin sulphate. This antibiotic is reported to be entirely effective in controlling bacilli introduced with the cultured *Artemia* nauplii used as food (Gilmour *et al.*, 1975). Gentle aeration was provided through a sintered glass block to keep both the larvae and *Artemia* circulating. *Artemia* eggs were hatched in 2 l of sea water with antibiotic in glass jars, and aerated vigorously for 48 h in an incubator at 25 °C. Five millilitres of newly hatched, concentrated nauplii were fed to the mass culture at each water change. To change the water the contents of the mass culture jar were poured gently through a 0·5 mm nylon mesh to retain the larvae which were then washed off into clean water. Each time the water was renewed, four larvae were preserved in 4% formalin.

The individual culture method used lidded trays of clear plastic with 18 compartments each of which holds 50 ml sea water with antibiotic. Two drops of concentrated *Artemia* nauplii were added, increasing to four drops as the larvae increased in size. The trays were examined every 2–3 days and any deaths or moults were recorded. Moults were pipetted out and preserved in formalin for subsequent examination.

Dissections were made in a 1 : 1 mixture of glycerine and 4% formalin under a Wild M5 microscope; a Wild M20 with camera lucida and phase contrast was used for drawings. Measurements of whole larvae were made from the tip of the rostrum to the base of the spines on the telson. In order to study morphological variation, especially of setal counts, flagellar segmentation and length ratios, all available material was examined at each zoeal stage. This included those larvae preserved regularly from mass cultures and all moults retained from the individual cultures. For each of the early zoeal stages up to 60 larvae and moults were examined and in later stages, even with mortality, at least 10 were examined.

Palaemon* (*Paleander*) *elegans Rathke, 1837

Palaemon elegans Rathke, 1837.
Leander squilla Czerniavsky, 1884.
Leander squilla elegans De Man, 1915.
Leander squilla intermedia De Man, 1915.
Leander squilla typica De Man, 1915.
Palaemon (*Paleander*) *elegans* Holthuis, 1950.

Synopsis of larval data from published work. *Leander squilla* Stuxberg, 1874 (zoea 1, plankton, Swedish waters); *Leander squilla* Keeble & Gamble, 1904 (zoea 1, chromatophores); *Leander squilla* Gurney 1924 (zoeae 1, 2 laboratory reared, not zoea 5 = post-larva, plankton, British waters); *Leander squilla elegans* Wimpenny & Titterington, 1936 (zoeae 1–6, post-larva, plankton, Lake Qarun, Egypt); *Leander squilla typica* Hoglund, 1943 (zoeae 1–6, post-larvae, plankton and laboratory reared, Swedish waters); *Palaemon elegans elegans* Tsurnamal, 1963 (zoeae 1–8, post-larva, laboratory reared, Israeli waters); *Palaemon elegans* Rochanaburanon & Williamson, 1976 (zoeae 1–9, post-larvae, laboratory reared, British waters).

In this paper, larvae employing thoracic appendage propulsion will be described as zoeae. Individuals using abdominal (pleopod) propulsion will be described as post-larvae and later, as juveniles, when all characters except secondary sexual characters of the adult are present (Williamson, 1969). In the following short descriptions of the key characters of the larval stages, all setal counts have been omitted but these are recorded in Table 2.

Description of larval stages.

Key characters are printed in *italic type*.

Zoea 1 (Fig. 2) 3·1 mm (2·8–3·2 mm)

Head (Figs 2a, b): *eyes sessile.*

Carapace (Figs 2a, b): *without spines*, *rostrum straight*, tapering distally, ventral margin with minute retrorse teeth distally.

Antenna 1 (Fig. 2c): peduncle bearing single flagellar segment with two aesthetascs distally.

Antenna 2 (Fig. 2d): exopodite (scaphocerite or antennal scale) as a broad lamina divided into four short segments distally.

Maxillipeds 1–3 (Figs 2h–j): with natatory exopodites.

Pereiopods 1, 2 (Figs 2k, l): *rudimentary*, *biramous. No trace of pereiopods 3–5.*

Abdomen (Figs 2a, b): somite 5 with posterior margin produced into a pair of short spines, *somite 6 continuous with telson.* No trace of pleopods.

Telson (Fig. 2m): fans out distally, posterior margin bears 7+7 plumose spines, with minute spines between four innermost pairs of spines.

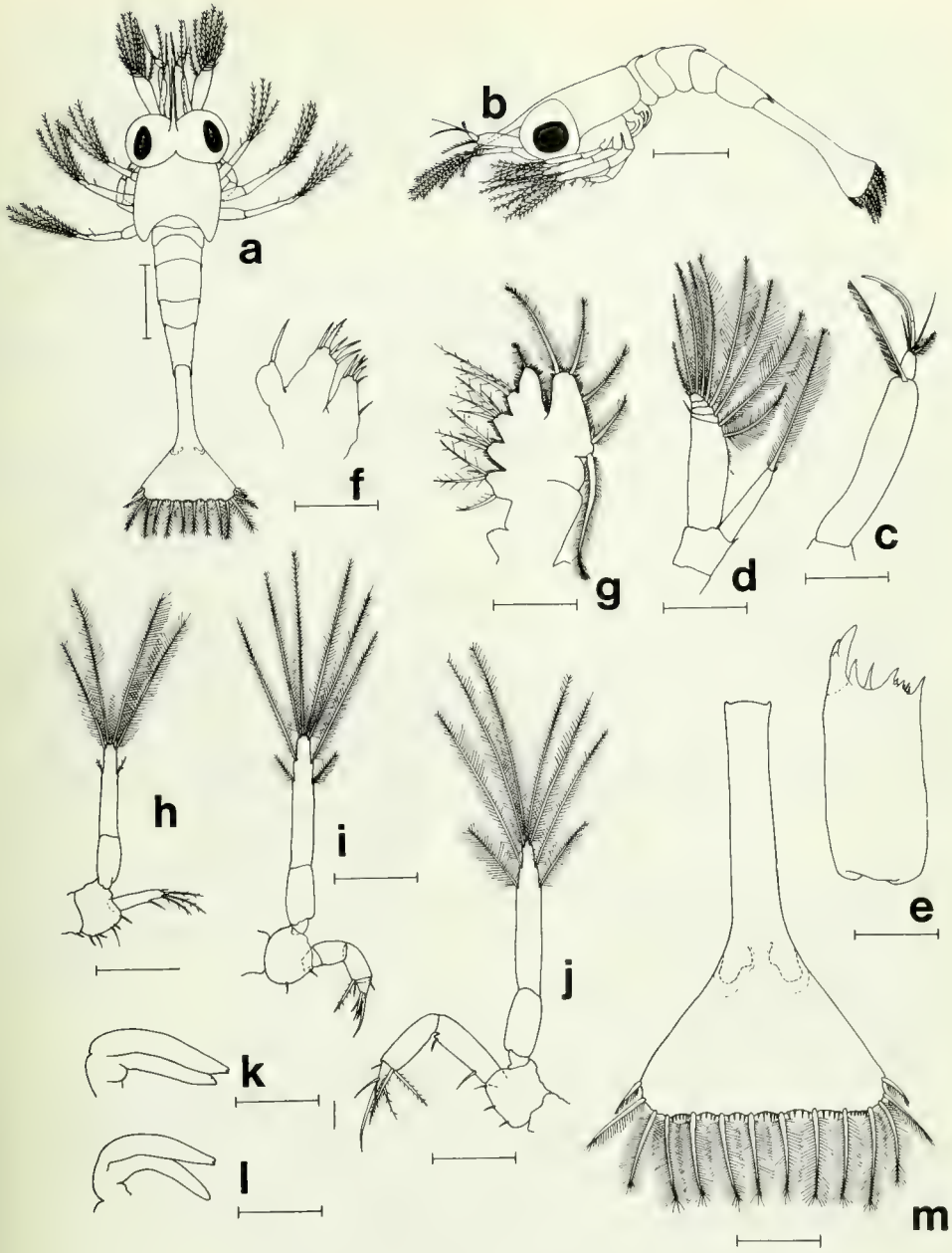

Fig. 2 Zoea 1: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandible; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) telson. Bar scales: a, b = 0·5 mm; c, d, h, i, j, k, l = 0·2 mm; g = 0·1 mm; e, f = 0·05 mm.

ZOEA 2 (Fig. 3) 3·2 mm (3·0–3·4 mm)

Head (Figs 3a, b): *eyes 'stalked'*.

Carapace (Figs 3a, b): *one dorso-medial and a pair of supraorbital spines* all bent forward with small retrorse teeth ventrally, *rostrum without teeth, downturned at end to form small hook*.

Pereiopods 1, 2 (Figs 3l, m): *developed, with natatory exopodites.*

Pereiopods 3, 4 (Figs 3n, o): *rudimentary, biramous.*

Pereiopod 5 (Fig. 3p): *rudimentary, uniramous* (without exopodite).

Telson (Fig. 3q): *developing uropods visible beneath exoskeleton*; in central group of small spines, one pair longer than the others.

ZOEA 3 (Fig. 4) 3·6 mm (3·3–3·8 mm)

Carapace (Figs 4a, b): *two dorso-medial spines* and a pair small frontolateral spines at edge of carapace beneath eyes, former with retrorse teeth ventrally.

Antenna 1 (Fig. 4c): conspicuous spine medially and stylocerite forming on proximal external margin of first segment of peduncle; distal segment of peduncle bearing first segment of internal flagellum.

Antenna 2 (Fig. 4d): exopodite with distal part divided into only two short segments.

Abdomen (Figs 4a, b): *somite six divided from telson by suture.*

Telson (Fig. 4p): narrower but still broader distally, outer pair of spines on posterior margin considerably reduced, *uropod endopodite with no marginal setae, exopodite with marginal plumose setae.*

ZOEA 4 (Figs 5, 6) 3·8 mm (3·4–4·1 mm)

Carapace (Figs 5a, b): *three dorso-medial spines* with small retrorse teeth ventrally, rostrum weakly hooked at apex.

Antenna 2 (Fig. 6b): endopodite three-quarters length of scaphocerite, distal part of exopodite no longer divided into short segments but with a stout, terminal spine on outer, distal edge.

Pereiopod 3 (Fig. 6h): *developed, with natatory exopodite.*

Pereiopod 4 (Fig. 6i): *rudimentary, biramous.*

Pereiopod 5 (Fig. 6j): *developed, uniramous.*

Telson (Fig. 6k): a little broader distally than proximally, posterior margin concave with 4+4 spines, *endopodite and exopodite of uropod both with marginal plumose setae.*

ZOEA 5 (Figs 7, 8) 4·5 mm (4·2–4·8 mm)

Antenna 1 (Fig. 7c): external flagellum with four distal aesthetascs.

Antenna 2 (Fig. 7d): endopodite with two-segmented flagellum, four-fifths length of scaphocerite (excluding setae).

Pereiopods 1, 2 (Figs 8d, e): *endopodite with internal distal margin of propodus produced slightly forward* (will become immobile finger of chela).

Pereiopod 4 (Fig. 8g): *developed, with natatory exopodite.*

Abdomen (Figs 7a, b): *somites 1–5 with rudimentary pleopods.*

Telson (Fig. 8i): subquadrate, posterior margin weakly concave.

ZOEA 6 (Figs 9, 10, 11) 5·2 mm (4·8–5·5 mm)

Carapace (Fig. 9b): *short plumose seta in angle of anterior dorso-medial spine*, rostrum straight or weakly hooked.

Antenna 2 (Fig. 9d): endopodite with three-segmented flagellum.

Pereiopods 1, 2 (Figs 10d, e): *endopodite with internal distal margin of propodus produced forward to over half length of dactylus* (excluding terminal setae).

Abdomen (Figs 9b, 10i–m): *pleopods on somites 1–5 rudimentary, biramous.*

Telson (Fig. 11a): wider medially than distally, posterior margin length about one-third overall length of telson.

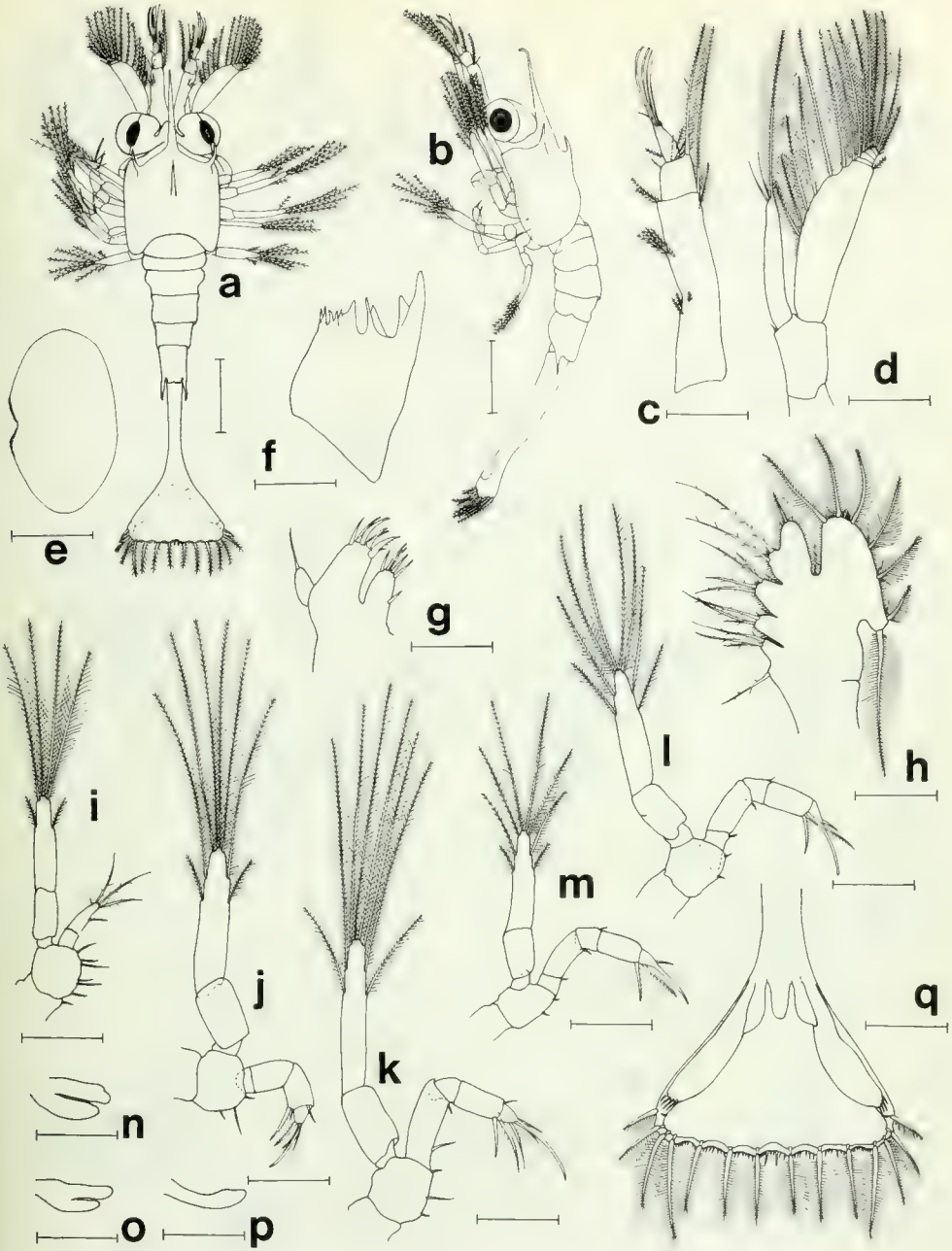

Fig. 3 Zoea 2: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) upperlip (labrum); (f) mandible; (g) maxilla 1; (h) maxilla 2; (i) maxilliped 1; (j) maxilliped 2; (k) maxilliped 3; (l) pereiopod 1; (m) pereiopod 2; (n) pereiopod 3; (o) pereiopod 4; (p) pereiopod 5; (q) telson. Bar scales: a, b = 0·5 mm; c, d, i, j, k, l, m, n, o, p, q = 0·2 mm; e, g, h = 0·1 mm; f = 0·05 mm.

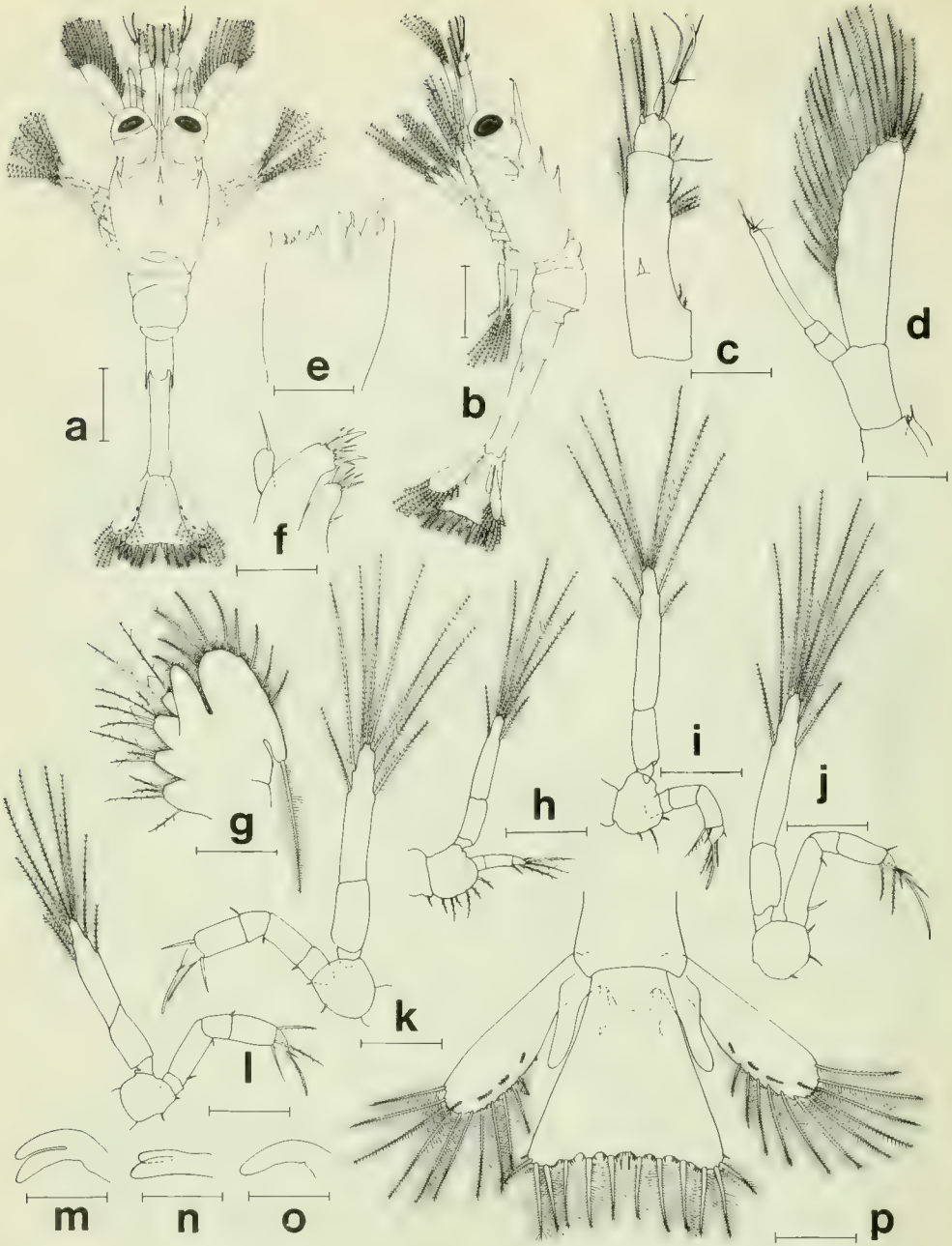

Fig. 4 Zoea 3: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandible; (f) maxilla 1; (g) maxilla 2; (h) maxilliped 1; (i) maxilliped 2; (j) maxilliped 3; (k) pereiopod 1; (l) pereiopod 2; (m) pereiopod 3; (n) pereiopod 4; (o) pereiopod 5; (p) telson. Bar scales: a, b = 0·5 mm; c, d, h, i, j, k, l, m, n, o, p = 0·2 mm; f, g = 0·1 mm; e = 0·05 mm.

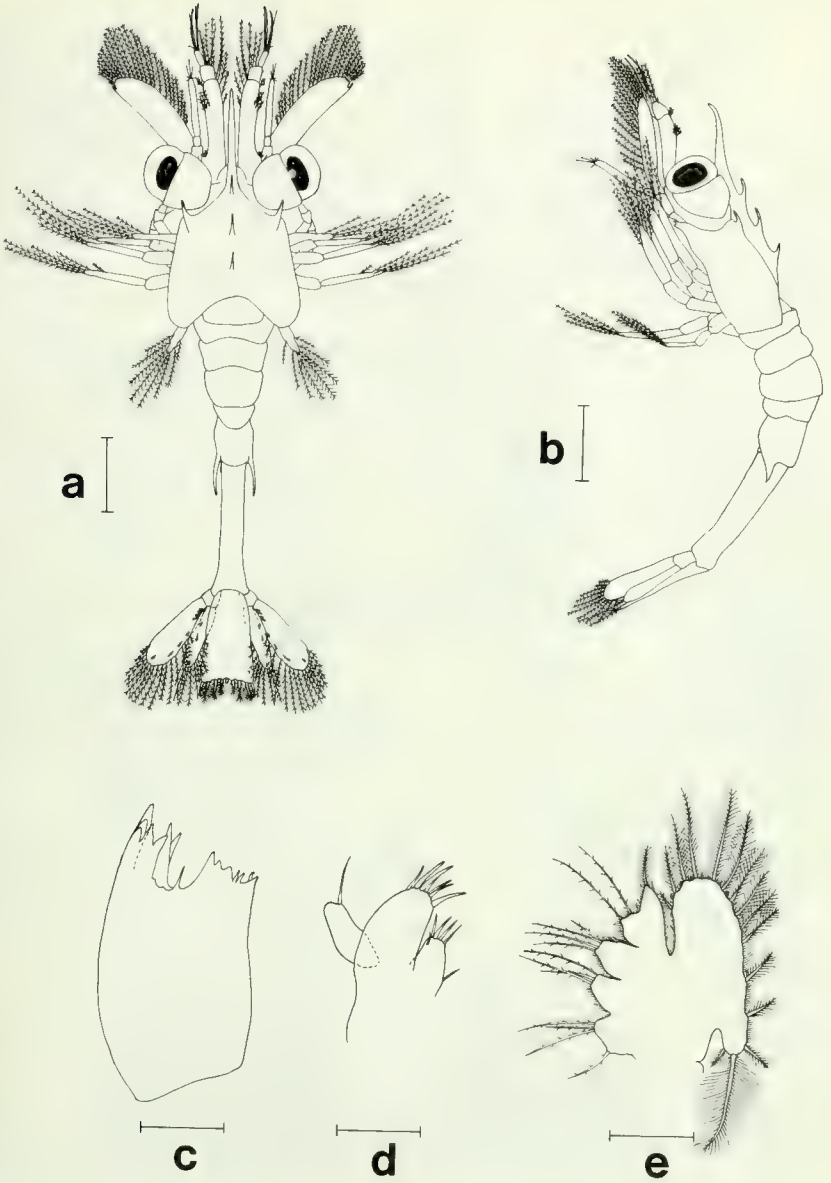

Fig. 5 Zoea 4: (a) dorsal view; (b) lateral view; (c) mandible; (d) maxilla 1; (e) maxilla 2. Bar scales: a, b = 0·5 mm; c = 0·05 mm; d, e = 0·1 mm.

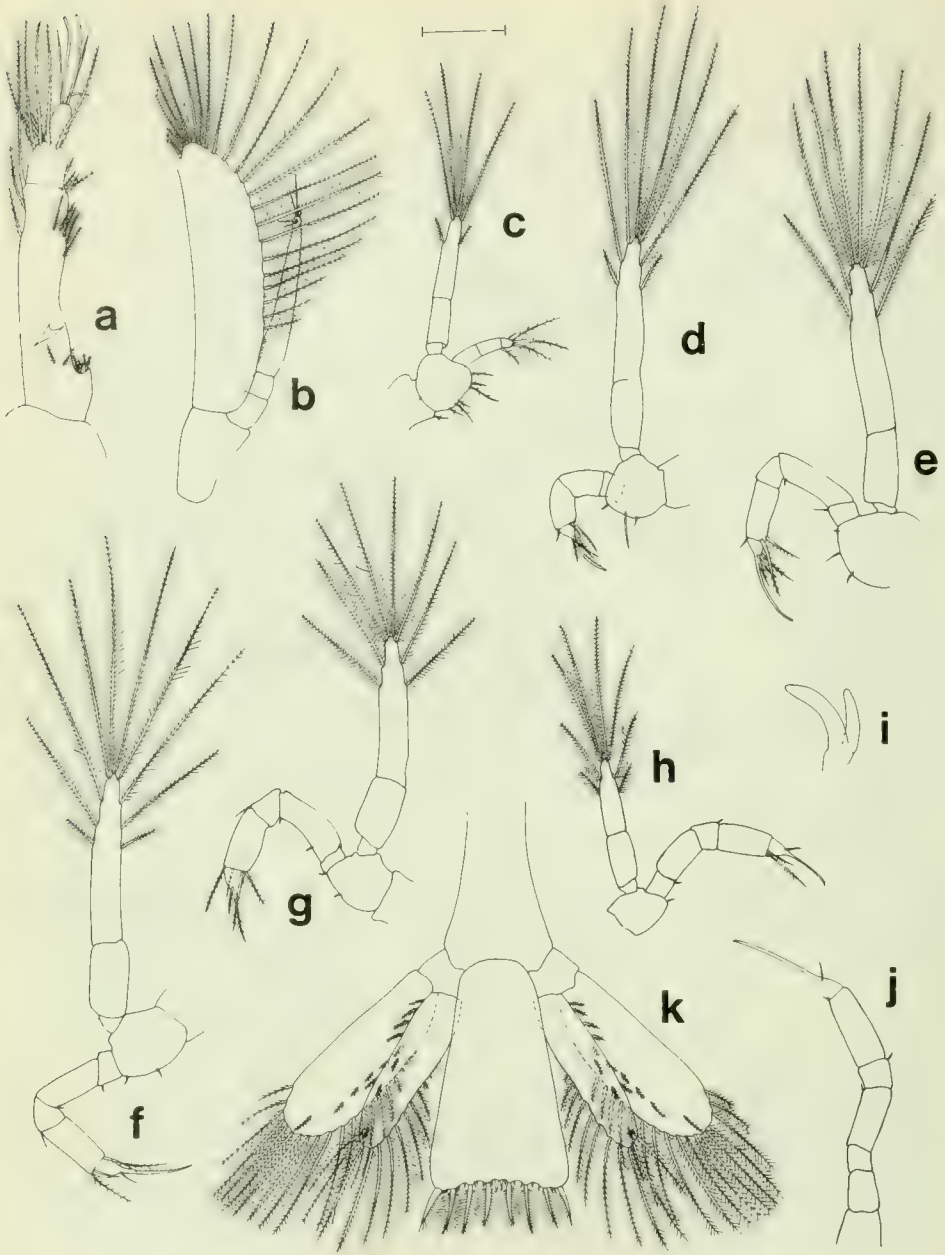

Fig. 6 Zoea 4: (a) antenna 1; (b) antenna 2; (c) maxilliped 1; (d) maxilliped 2; (e) maxilliped 3; (f) pereiopod 1; (g) pereiopod 2; (h) pereiopod 3; (i) pereiopod 4; (j) pereiopod 5; (k) telson. Bar scale: a–k = 0·2 mm.

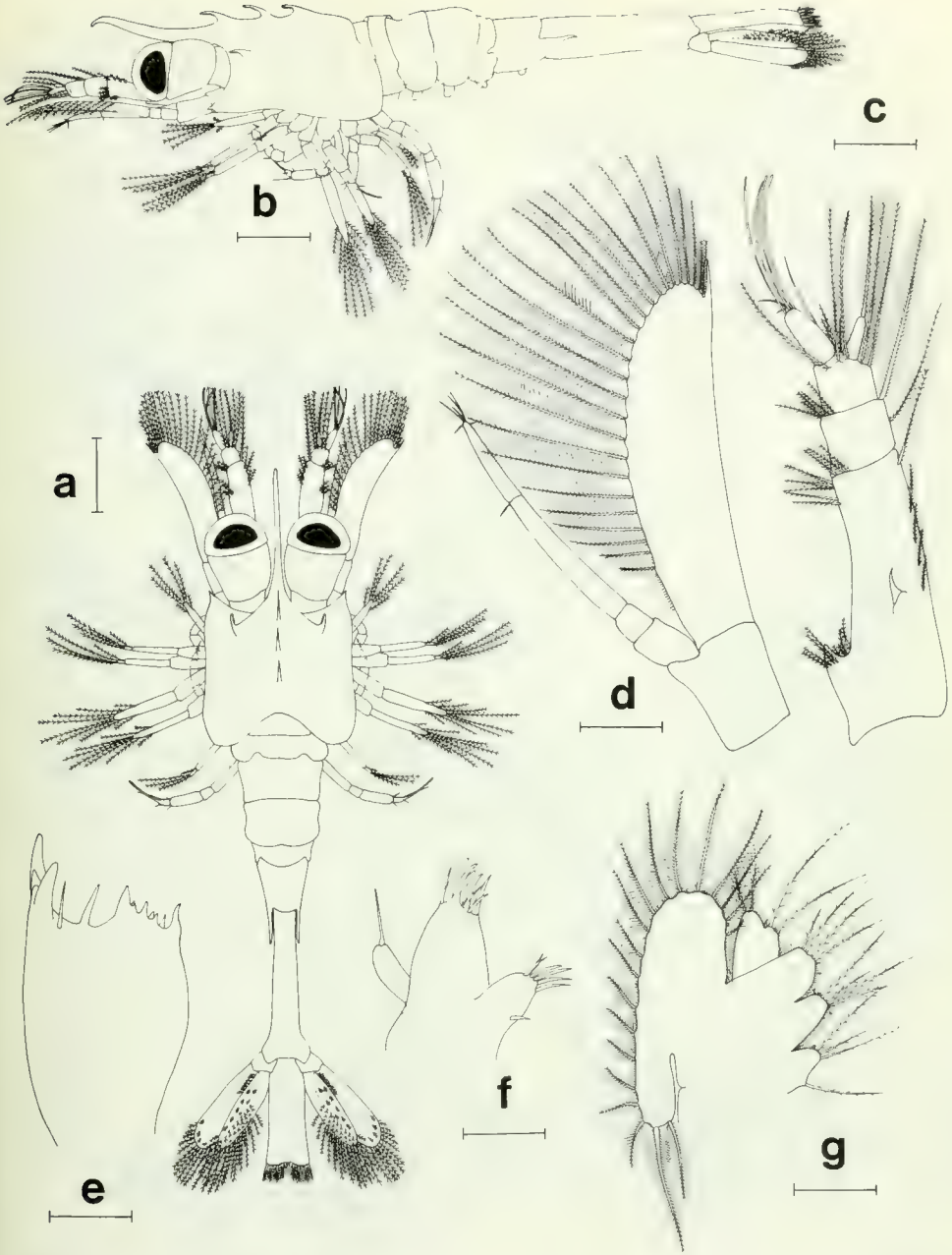

Fig. 7 Zoea 5: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandible; (f) maxilla 1; (g) maxilla 2. Bar scales: a, b = 0·5 mm; c, d = 0·2 mm; e = 0·05 mm; f, g = 0·1 mm.

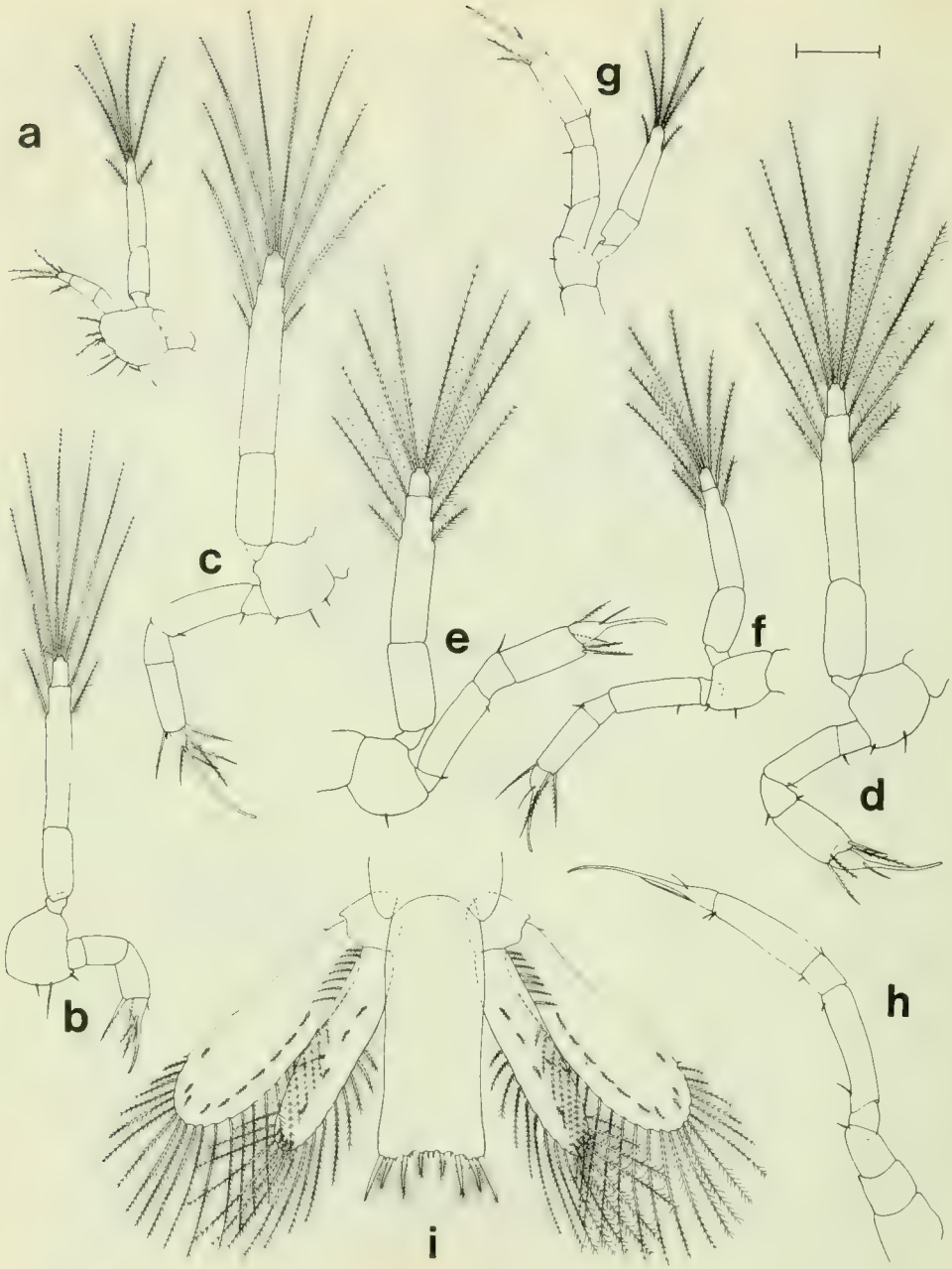

Fig. 8 Zoea 5: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1; (e) pereiopod 2; (f) pereiopod 3; (g) pereiopod 4; (h) pereiopod 5; (i) telson. Bar scale: a–i = 0·2 mm.

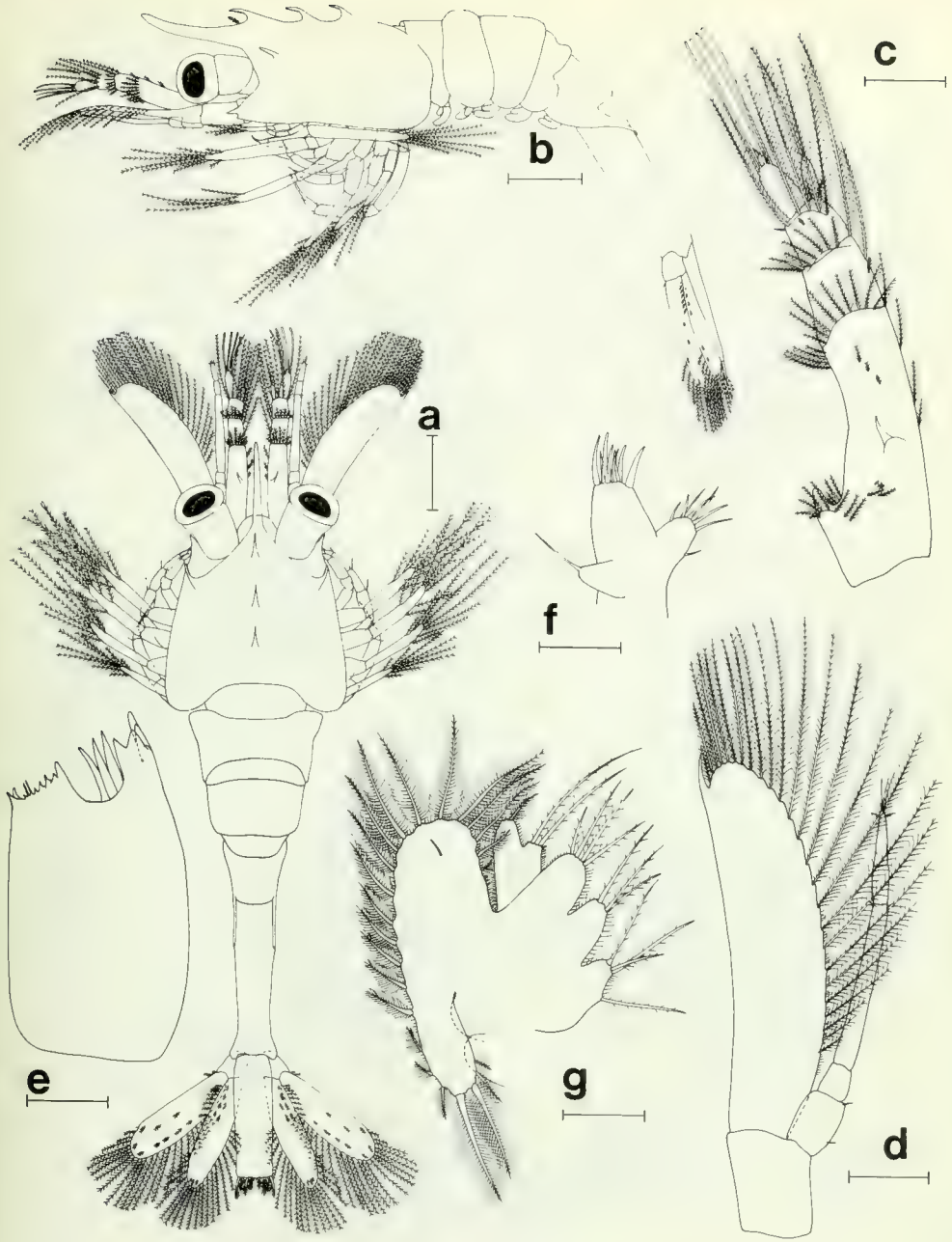

Fig. 9 Zoea 6: (a) dorsal view; (b) lateral view; (c) antenna 1; (d) antenna 2; (e) mandible; (f) maxilla 1; (g) maxilla 2. Bar scales: a, b = 0·5 mm; c, d = 0·2 mm; e = 0·05 mm; f, g = 0·1 mm.

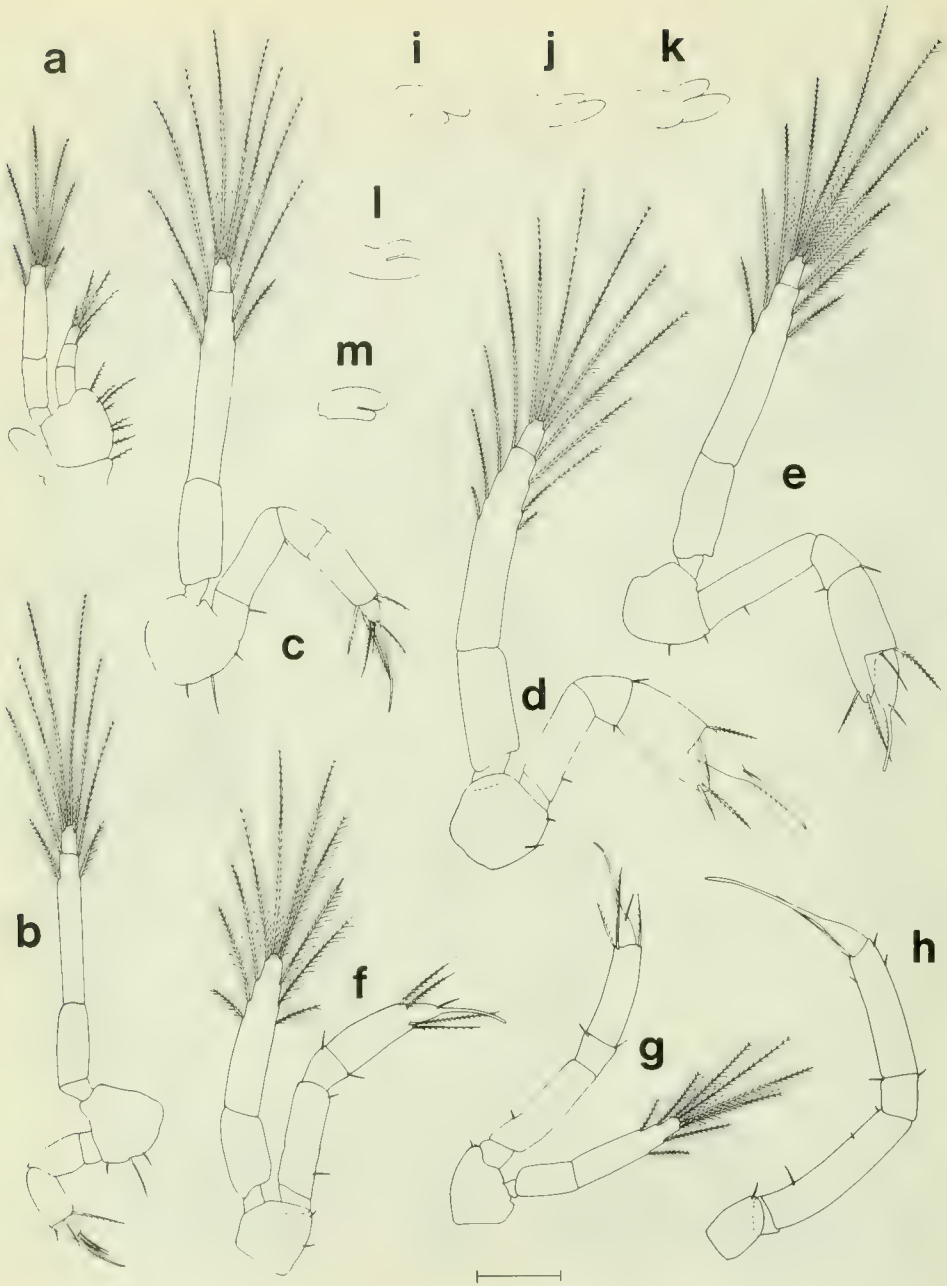

Fig. 10 Zoea 6: (a) maxilliped 1; (b) maxilliped 2; (c) maxilliped 3; (d) pereiopod 1; (e) pereiopod 2; (f) pereiopod 3; (g) pereiopod 4; (h) pereiopod 5; (i) pleopod 1; (j) pleopod 2; (k) pleopod 3; (l) pleopod 4; (m) pleopod 5. Bar scale: a–m = 0·2 mm.

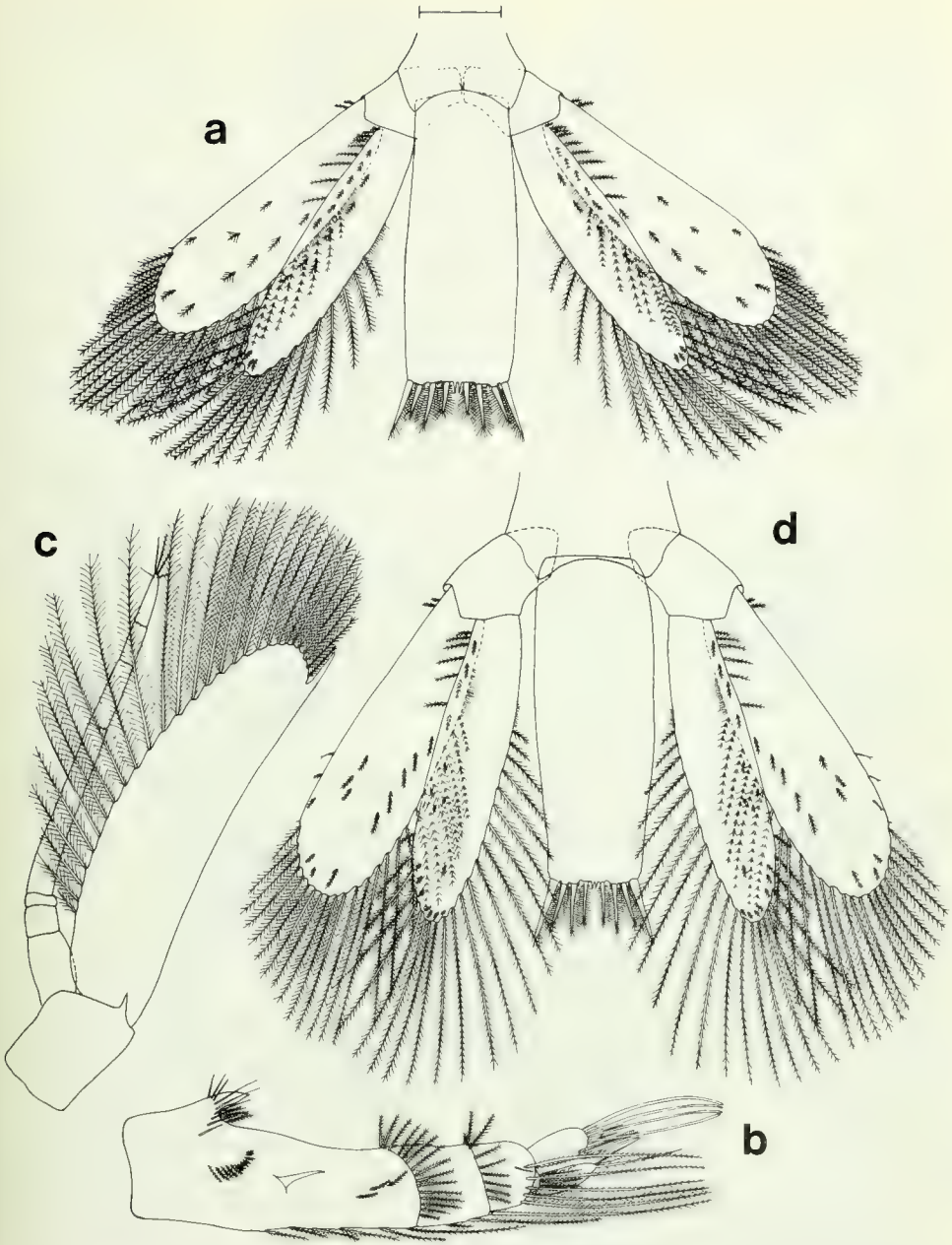

Fig. 11 Zoea 6: (a) telson. Zoea 7: (b) antenna 1; (c) antenna 2; (d) telson. Bar scale: a–d = 0·2 mm.

ZOEA 7 (Fig. 11)

Similar in most characters to zoea 6 with the following exceptions:

Antenna 1 (Fig. 11b): circlet of plumose setae developed dorsally on first segment of peduncle, indicating position of statocyst, additional group of three aesthetascs on external flagellum.

Antenna 2 (Fig. 11c): *increase in number of segments of endopodite flagellum, approximately equal to scaphocerite in length.*

Telson (Fig. 11d): slightly narrower distally.

ZOEA 8 (Figs 12, 13, 14, 15) 6·4 mm (6·0–6·6 mm)

Carapace (Fig. 12b): *three short setae in angle of anterior dorso-medial spine, rostrum no longer hooked.*

Antenna 1 (Fig. 12c): external flagellum of two segments, further group of two aesthetascs added proximal to other two groups.

Antenna 2 (Fig. 13a): *flagellum of exopodite multisegmented, just longer than scaphocerite.*

Pereiopods 1, 2 (Figs 14a, b): *endopodite with immovable finger of propodus produced forward to almost length of dactylus* (excluding terminal setae).

Abdomen (Figs 12b, 13h–l): *pleopods with rudimentary setae on margins of endopodite* (except pleopod 1) and exopodite, endopodite of pleopods 2–5 with rudiment of appendix interna (stylamblys).

Telson (Fig. 15a): narrowing distally, *posterior margin convex*, pair of small spines at distal corners.

ZOEA 9 (Figs 15, 16, 17) 7·4 mm (7·0–8·0 mm)

Carapace (Fig. 16b): *five setae in angle of anterior dorso-medial spine.*

Antenna 1 (Fig. 15c): internal flagellum of three segments, additional group of two aesthetascs proximally on first segment of external flagellum.

Antenna 2 (Fig. 15d): *endopodite with flagellum approximately 1·5 times length of scaphocerite.*

Abdomen (Figs 17g–k): *pleopods with some plumose setae on margins of exopodites.*

Telson (Fig. 15b): further narrowing distally, *no small spines between large spines.*

POST-LARVA 1 (Figs 18, 19, 20) 7·9 mm (7·5–8·4 mm)

Carapace (Fig. 19a): *rostrum usually with eight* (7–9) *dorsal and two ventral spines, supraorbital spines missing.*

Antenna 2 (Fig. 18b): *endopodite twice length of scaphocerite*, about 27 segments.

Mandible (Fig. 18c): *divided into pars incisiva and pars molaris*, lacinia mobilis no longer present and palp (two-jointed in adult) not yet appeared.

Maxilliped 2 (Fig. 19c): endopodite with dactylus and merus flattened, *exopodite shortened and with no setae.*

Maxilliped 3 (Fig. 20d): endopodite dactylus shortened, *exopodite reduced* to less than the length of ischium and merus of endopodite, and without setae.

Pereiopod 1 (Fig. 19e): merus and carpus lengthened, *exopodite reduced* (less than length of basis and ischium) with a few degenerate plumose setae.

Pereiopod 2 (Fig. 19f): as for pereiopod 1 except *exopodite reduced* to about length of the basis and no setae.

Pereiopods 3, 4 (Figs 19g, h): endopodite dactylus shortened, merus carpus and propodus lengthened, *exopodite reduced*, extending half-way along ischium of endopodite and with no setae.

Pereiopod 5 (Fig. 19i): shortening of dactylus, all other segments of endopodite lengthened.

Pleopod 1 (Fig. 20a): ratio of endopodite to exopodite 1 : 4·5, *endopodite bearing terminal plumose setae, exopodite fringed with long plumose setae.*

Pleopods 2–5 (Figs 20b–e): endopodite over half the length of exopodite both with long, marginal, plumose setae, endopodite with appendix interna bearing well-developed intero-distal coupling hooks.

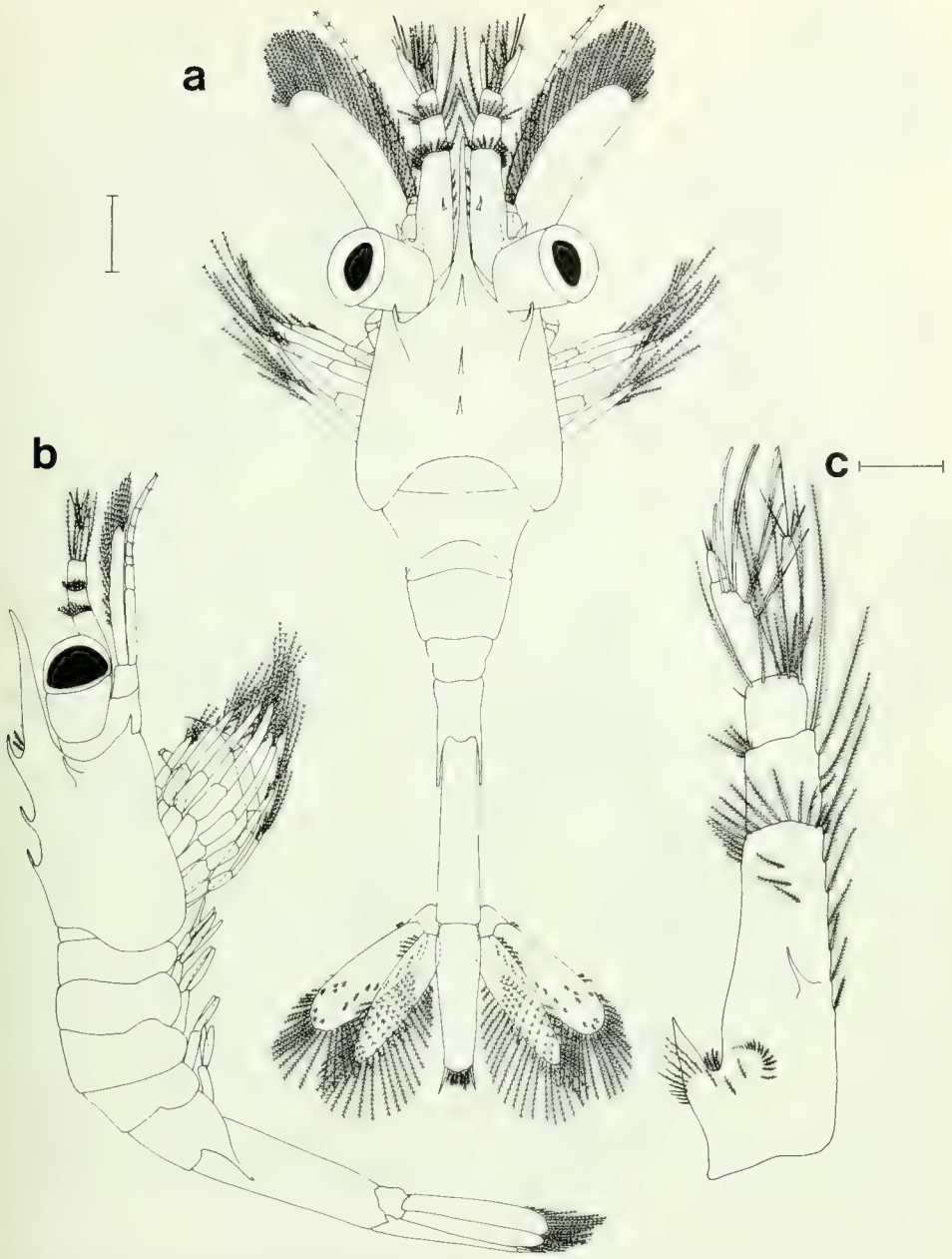

Fig. 12 Zoea 8: (a) dorsal view; (b) lateral view; (c) antenna 1. Bar scales: a, b = 0·5 mm; c = 0·2 mm.

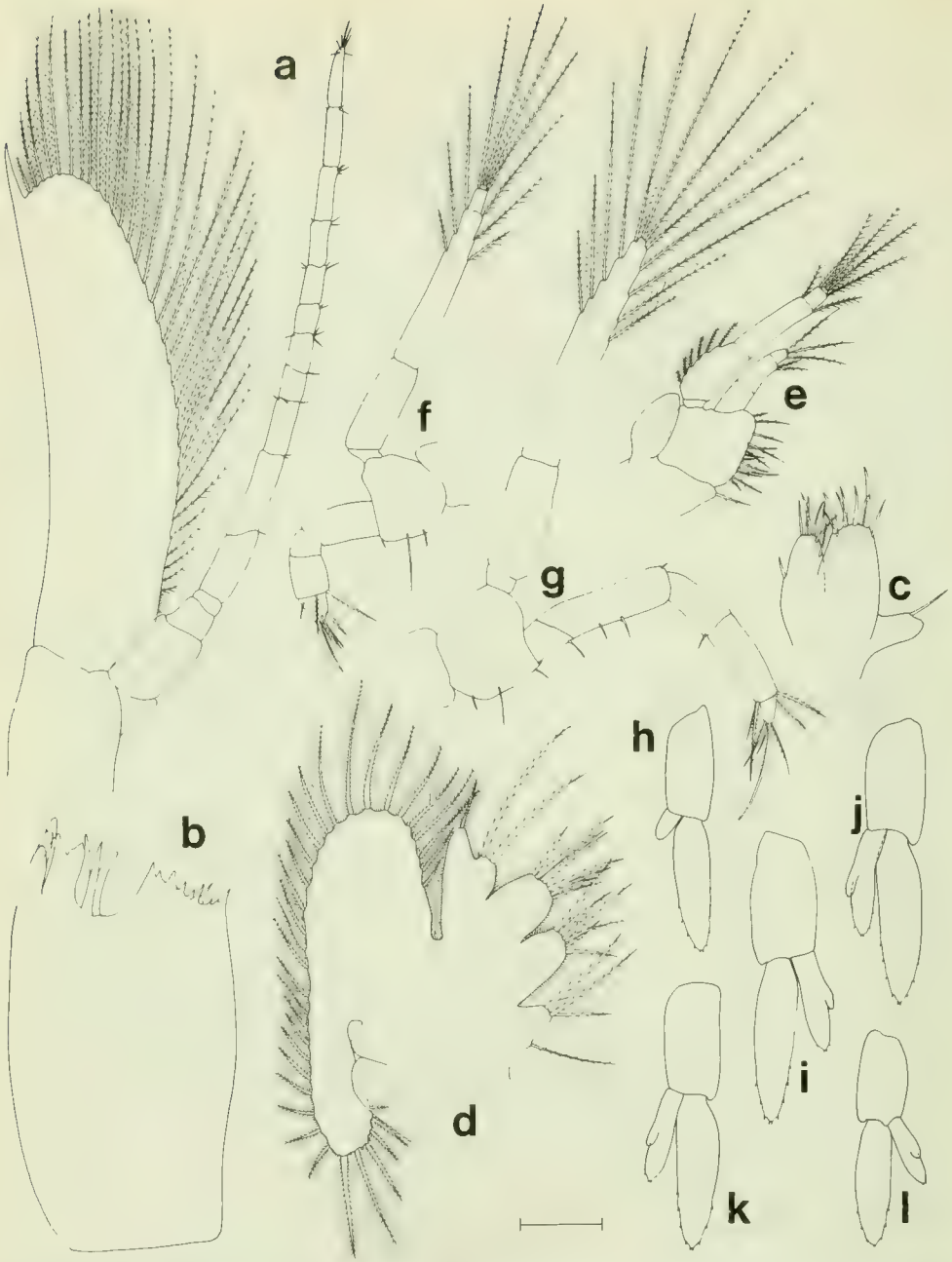

Fig. 13 Zoea 8: (a) antenna 2; (b) mandible; (c) maxilla 1; (d) maxilla 2; (e) maxilliped 1; (f) maxilliped 2; (g) maxilliped 3; (h) pleopod 1; (i) pleopod 2; (j) pleopod 3; (k) pleopod 4; (l) pleopod 5. Bar scale: a, e–l = 0·2 mm; b = 0·05 mm; c, d = 0·1 mm.

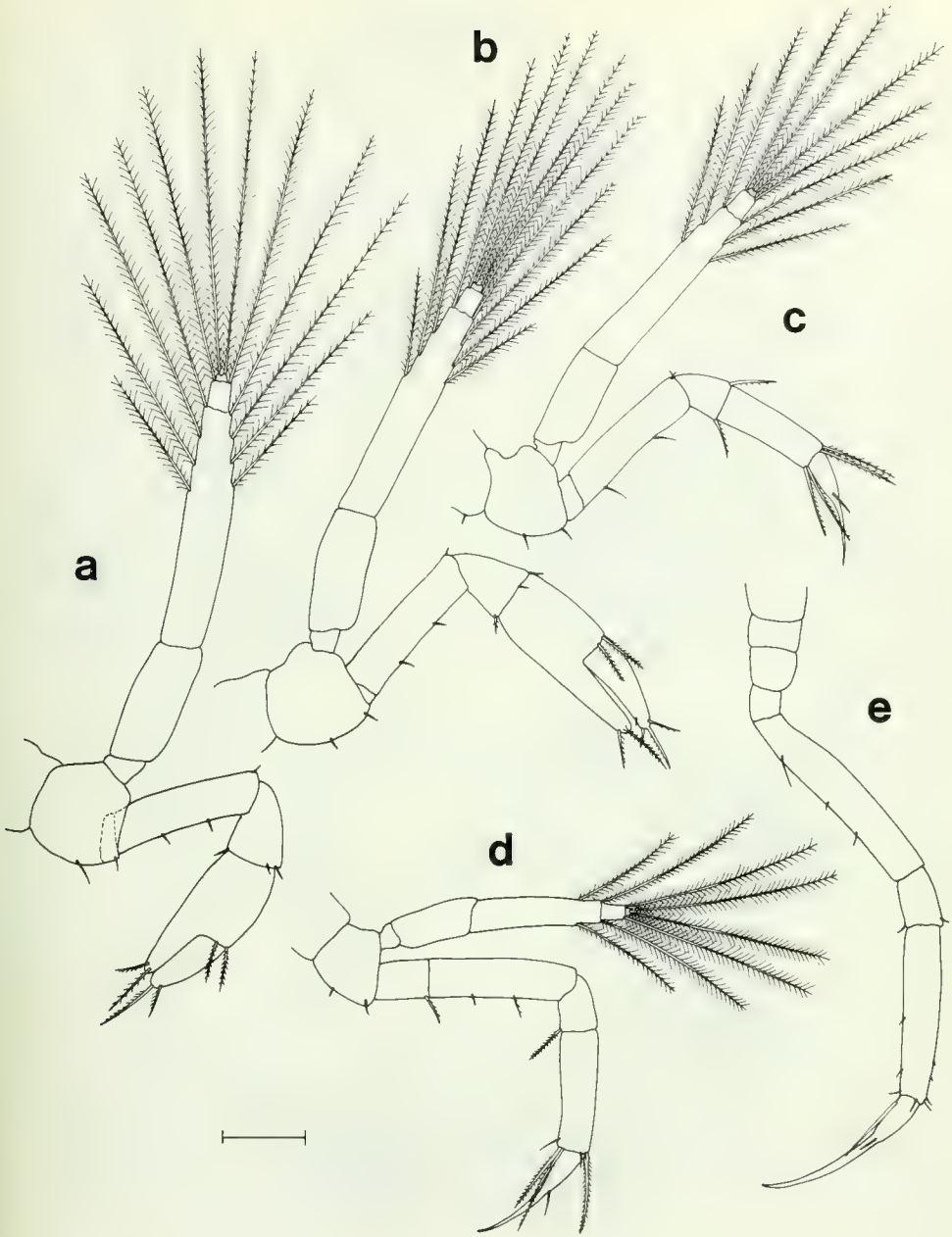

Fig. 14 Zoea 8: (a) pereiopod 1; (b) pereiopod 2; (c) pereiopod 3; (d) pereiopod 4; (e) pereiopod 5. Bar scale: a–e = 0·2 mm.

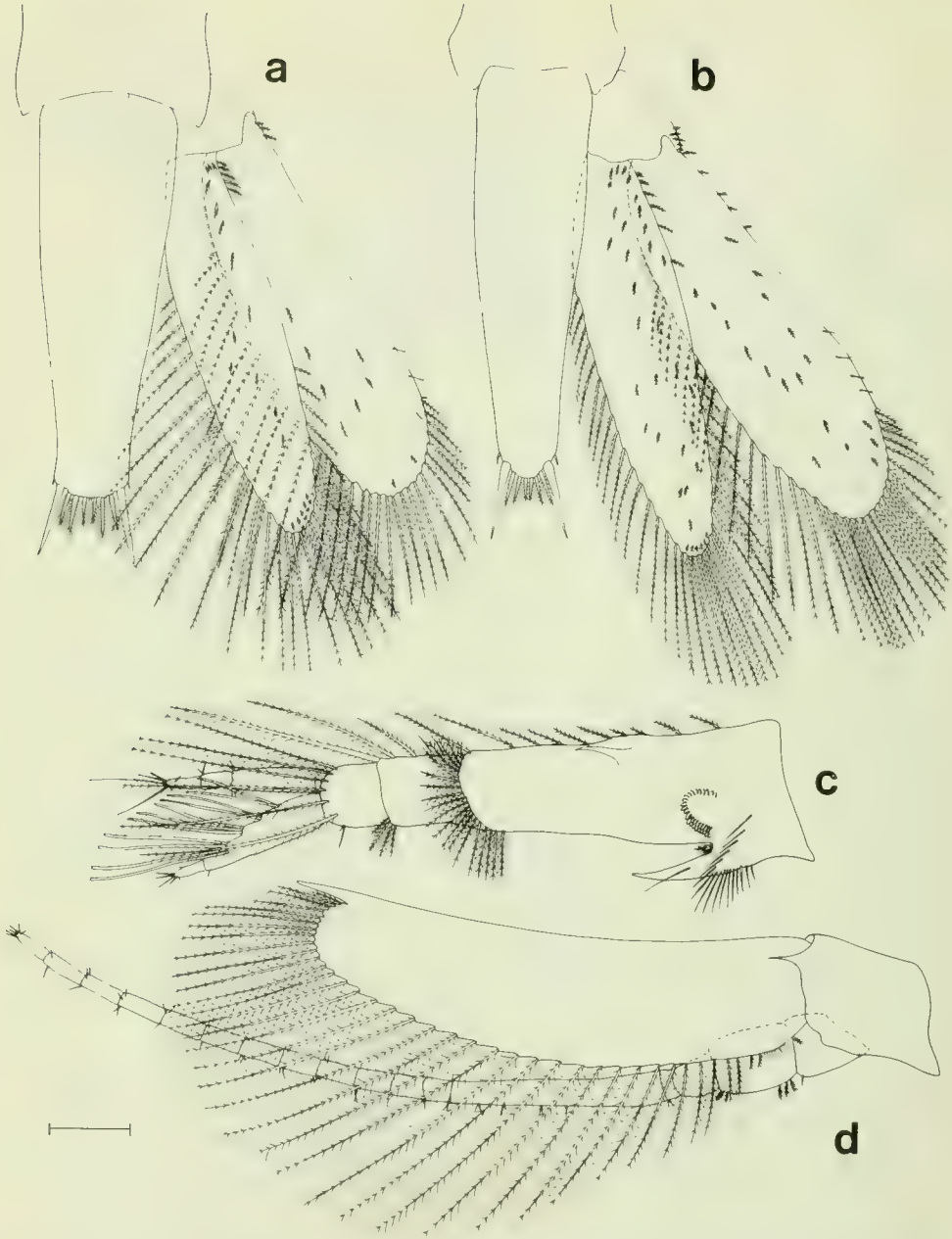

Fig. 15 Zoea 8: (a) telson. Zoea 8: (b) telson; (c) antenna 1; (d) antenna 2. Bar scale: a–d = 0·2 mm.

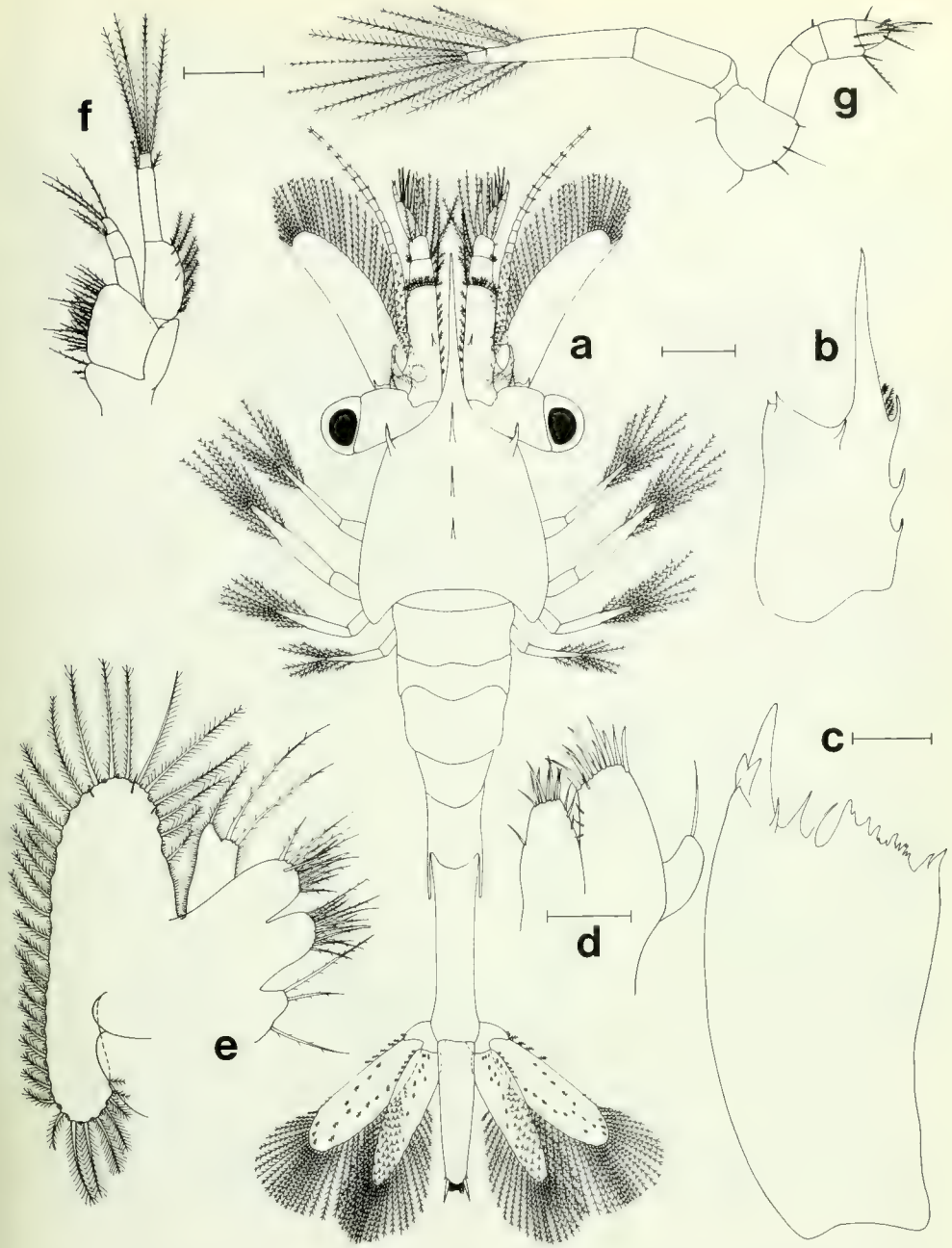

Fig. 16 Zoea 9: (a) dorsal view; (b) lateral view of carapace; (c) mandible; (d) maxilla 1; (e) maxilla 2; (f) maxilliped 1; (g) maxilliped 2. Bar scales: a, b = 0·5 mm; c = 0·05 mm; d, e = 0·1 mm; f, g = 0·2 mm.

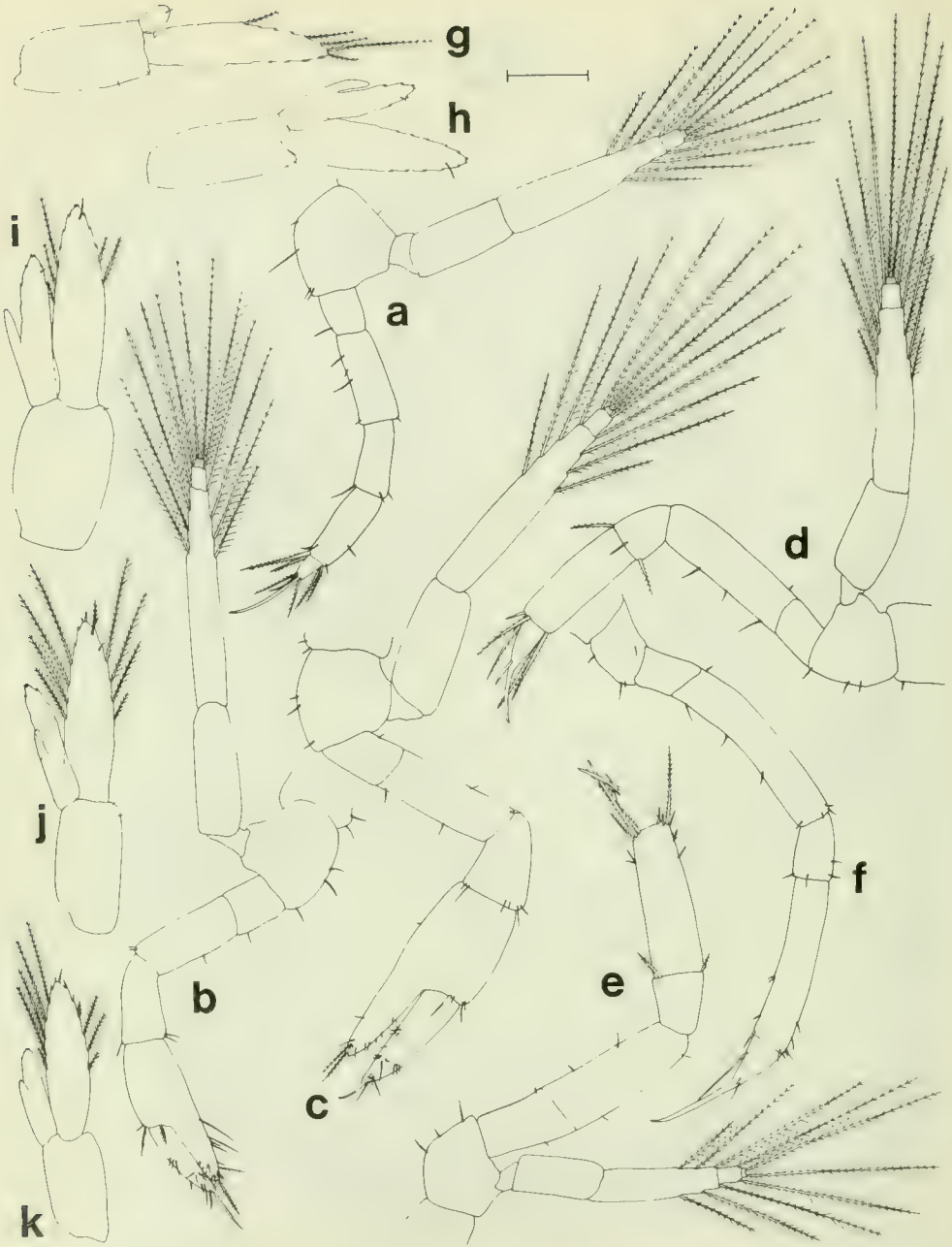

Fig. 17 Zoea 9: (a) maxilliped 3; (b) pereiopod 1; (c) pereiopod 2; (d) pereiopod 3; (e) pereiopod 4; (f) pereiopod 5; (g) pleopod 1; (h) pleopod 2; (i) pleopod 3; (j) pleopod 4; (k) pleopod 5. Bar scale: a–k = 0·2 mm.

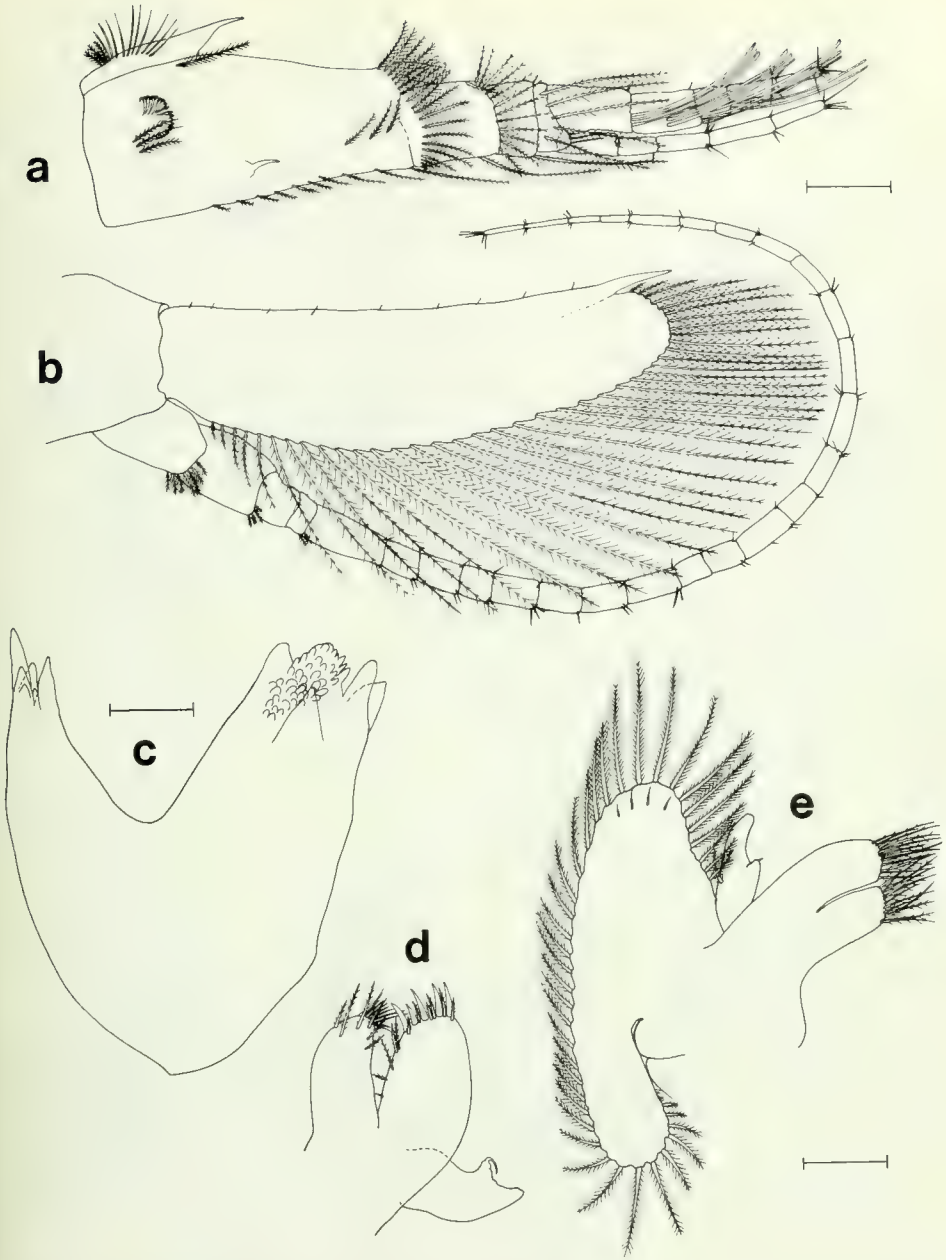

Fig. 18 Post-larva 1: (a) antenna 1; (b) antenna 2; (c) mandible; (d) maxilla 1; (e) maxilla 2. Bar scales: a, b = 0·2 mm; c = 0·05 mm; d, e = 0·1 mm.

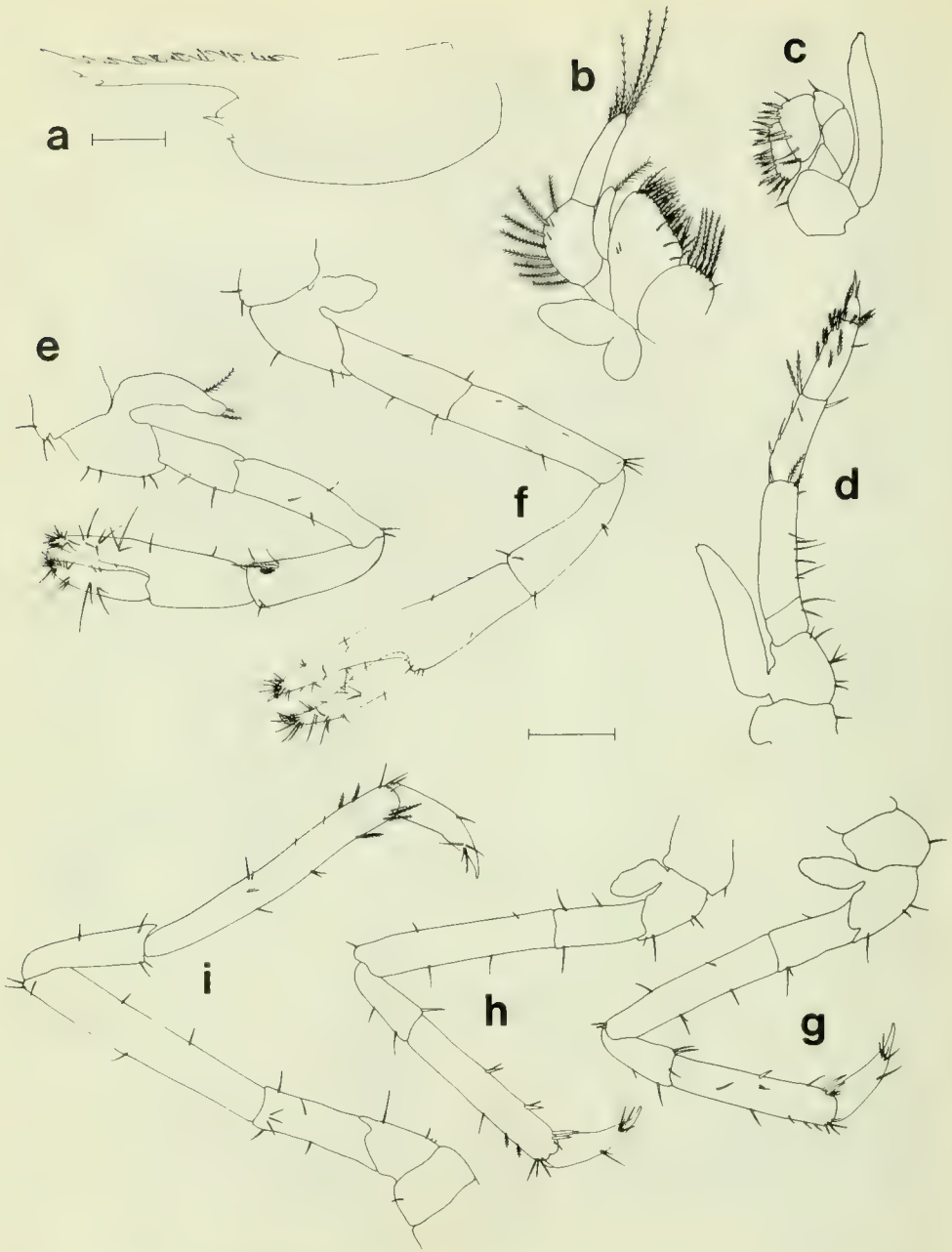

Fig. 19 Post-larva 1: (a) lateral view of carapace; (b) maxilliped 1; (c) maxilliped 2; (d) maxilliped 3; (e) pereiopod 1; (f) pereiopod 2; (g) pereiopod 3; (h) pereiopod 4; (i) pereiopod 5. Bar scales: a = 0·5 mm; b–i = 0·2 mm.

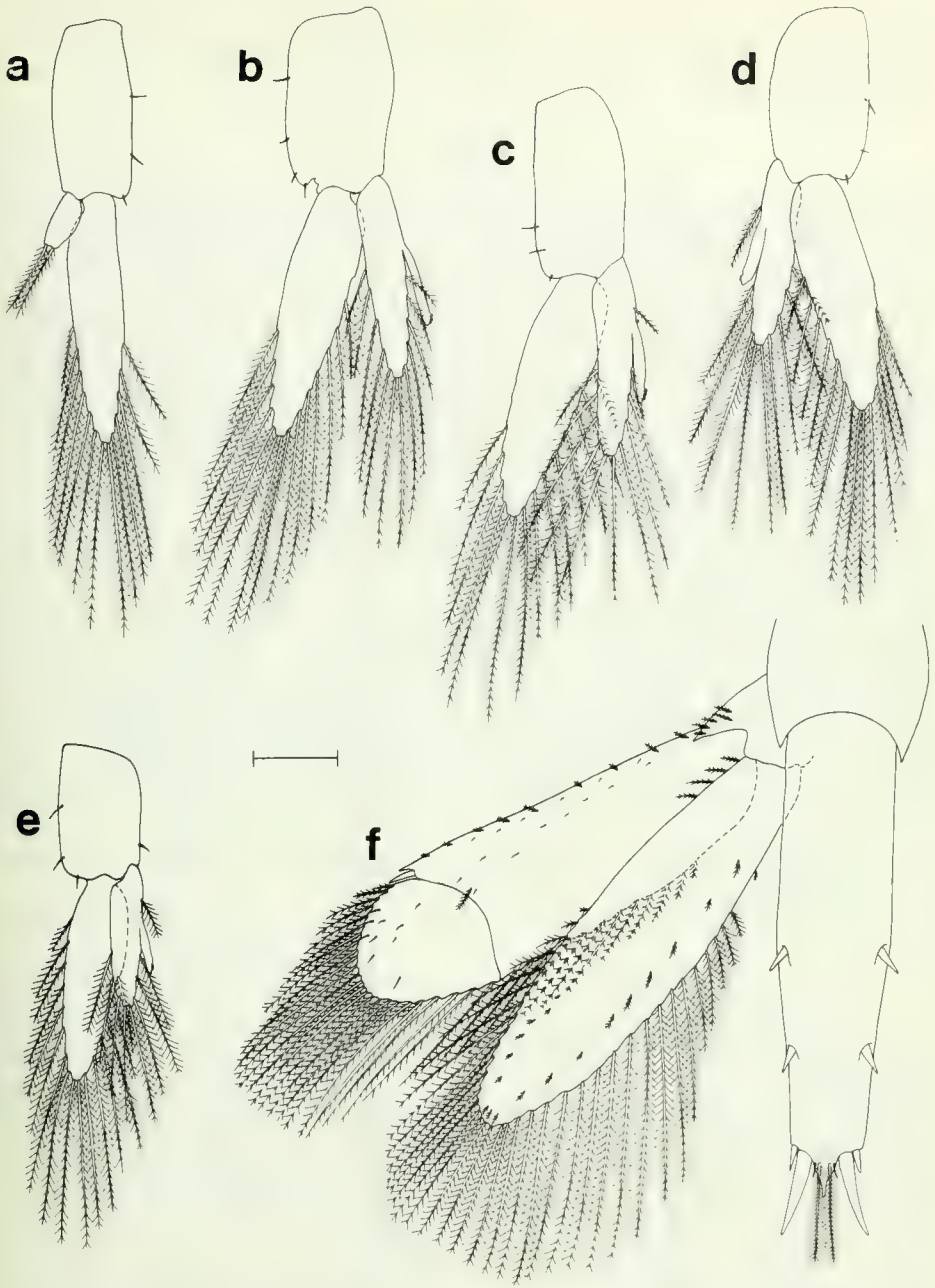

Fig. 20 Post-larva 1: (a) pleopod 1; (b) pleopod 2; (c) pleopod 3; (d) pleopod 4; (e) pleopod 5; (f) telson. Bar scale: a–f = 0·2 mm.

Abdomen: *fifth abdominal somite rounded on lateral margins* and not extending to a point as in previous stages.

Telson (Fig. 20f): *extremely narrow, posterior margin tapering to a point* and bearing a pair of small (outer) and large (inner) spines and medially a pair of short, simple and a pair of plumose setae. Two pairs of stout spines developed on lateral margins of telson, *uropod exopodite divided into two parts by suture.*

Discussion

Results of previous workers and of the present study are summarized in Tables 1 and 2 from which a number of interesting points emerge. Zoeae in northern waters increase in length faster than their Mediterranean counterparts until the first post-larval stage (PL1) is reached after which the situation is reversed. One particularly interesting feature of the metamorphosis to PL1 is that the natatory exopodites of pereiopods 1–4 disappear (with a stronger tendency to degeneration in the northern forms as noticed by Tsurnamal, 1963). There is also a temporary regression of the exopodites of maxillipeds 2 and 3 in which the marginal plumose setae are lost and the exopodites shorten. In subsequent moults, PL1 and PL2, these plumose setae are restored and the exopodites of the maxillipeds lengthen, but the pereiopods remain uniramous. It is possible that the temporary regression of exopodites of maxillipeds 2 and 3 together with other morphological changes at metamorphosis to post-larva are under the same hormone control. Hopefully, subsequent papers in this series will provide more data on these morphogenetic changes and associated modifications in swimming and feeding behaviour.

Compared with the growth of pereiopods 3–5, that of pereiopods 1 and 2 is remarkably rapid as the rudimentary biramous buds of these become fully formed pereiopods in zoea 2 with propodus extension into fixed finger of chela beginning in zoea 4 or 5 and finally the loss of the exopodite at PL1. Uniramous pereiopod 5 first appears in rudimentary form in zoea 2, before becoming 5-segmented at zoea 4; at no stage does it have an exopodite.

The changes which occur from final zoea to PL1 are dramatic and easily identifiable; the first five zoeae are also morphologically distinct. In those examples where there are only six larval stages then zoea 6 is also clearly defined. When extra moults are inserted, however, between zoeae 5 and 6, distinction between the moults is less clearly defined and considerable overlap occurs in the number of setae on appendages in successive moults. This makes the recognition of morphological stages beyond moult 5 problematical. The situation is confused by the insertion

Table 1 Lengths (mm) of zoeae and post-larvae 1 of *Palaemon* (*Paleander*) *elegans* throughout its geographical range.

Stages	Gurney, 1924 England	Wimpenny & Titterington, 1936 Egypt	Hoglund, 1943 Sweden	Tsurnamal, 1963 Israel	Rochanaburanon, 1974; Rochanaburanon & Williamson[1], 1976 Isle of Man	Present work England
1	3·0–3·2	2·8–3·1	2·6–2·8	2·2–2·8	3·0–3·1	2·8–3·2
2	3·17–3·7	2·7–3·4	3·4–3·7	2·9–3·2	3·5–3·7	3·0–3·4
3		3·0–3·8	4·0–4·5	3·6–3·75	3·9–4·1	3·3–3·8
4		3·2–4·5	4·75–5·25	4·1–4·6	4·7–4·8	3·4–4·1
5		3·9–5·0	5·8–6·9	4·3–5·4	5·6–5·8	4·2–4·8
6		5·4–7·6	6·9–7·4	6·0–6·6	6·1–6·7	4·8–5·5
7				6·5–6·71		6·0–6·6
8				6·5–6·75		6·0–6·6
9						7·0–8·0
PL1	7·86	8·9–9·4	7·4–8·0	6·7–7·0	6·3–7·9	7·5–8·4

[1] Carapace characters PL1 not included in Table 2. Number of rostral spines: dorsal 7–9 and ventral 1–3.

Table 2 Comparison of structure in larval d

		Present work England								
	PL1	1	2	3	4	5	6	7 & 8	9	PL1
Carapace										
No. of dorsal spines	7–9	0	1	2	3	3	3	3	3	7–9
No. of ventral rostral spines	2	0	0	0	0	0	0	0	0	2
Supraorbital spines +/−	−	−	+	+	+	+	+	+	+	−
No. of antero-lateral spines	2	0	0	2	2	2	2	2	2	2
Rostrum tip – Downturned +/−	−	−	+	+	+/−	+/−	+/−	−	−	−
Ventral retrorse hooks +/−	−	+	−	−	−	−	−	−	−	−
Antenna 1										
No. of groups, Aesthetascs	3	1	1	1	1	2	3	4	4	4
Stylocerite +/−	+	−	−	+	+	+	+	+	+	+
Statocyst +/−		−	−	−	−	−	−	+	+	+
No. of segments, Flagellum – Internal	5–6	0	0	1	1	1	1	1	3	5
External	5	1	1	1	1	1	1	2	2	5
Accessory flagellum +/−	+	−	−	−	−	−	−	−	−	+
Antenna 2										
Endopodite – No. of segments	33	1	1	3	3	4	5	14	16	29
Length of scaphocerite	4·0	0·50	0·66	0·66	0·75	0·80	0·80	1·2	1·50	2·00
Exopodite – No. of distal segments	0	4	4	2	0	0	0	0	0	0
No. of plumose setae	35–37	9	14–16	17–20	21–22	23–26	25–29	29–34	36	36–40
External spine +/−	+	−	−	−	+	+	+	+	+	+
Mandible – Lacinia mobilis +/−	−	+	+	+	+	+	+	+	+	−
Palp +/−	−	−	−	−	−	−	−	−	−	−
Maxilla 1										
No. of endite setae – Coxa	18	6	6	6	6	7	8	8	15	17
Basis	16	5	7	7	7	8	8	8	11	16
Maxilla 2										
No. of endite setae – Coxa	0	4	4	4	4	4	4	4	3	0
Basis 1	9	4	4	4	4	4	4	7	12	12
2	9	3	3	3	3	3–4	3–4	6	12	12
Endopodite	0	2	2	2	2	2	2	2	2	0
No. of plumose setae, Exopodite	42–43	5	7	9–11	13–15	16–21	20–24	34	36	40
Maxilliped 1										
No. of setae on internal margin – Coxa		1	1	1	1	1	1	1	3	11
Basis		6	6	6	6	7	7	13	27	31
Exopodite, No. of setae – Lateral (proximal)		0	0	0	0	0	0	6	8	8
Maxilliped 2										
Endopodite – No. of segments	+	4	4	4	4	4	4	4	4	5
Exopodite +/−	−	+	+	+	+	+	+	+	+	+
Setae +/−		+	+	+	+	+	+	+	+	−
Maxilliped 3										
Endopodite – No. of segments	4	3	4	4	5	5	5	5	5	5
Exopodite +/−	+	+	+	+	+	+	+	+	+	+
Setae +/−	−	+	+	+	+	+	+	+	+	−
Pereiopods 1 and 2 +/−	+	R+	+	+	+	+	+	+	+	+
Biramous +/−	−	+	+	+	+	+	+	+	+	−
Endopodite – Propodus fixed finger +/−	+	−	−	−	−	+	+	+	+	+
Pereiopod 3 +/−	+	−	R+	R+	+	+	+	+	+	+
Biramous +/−	−		+	+	+	+	+	+	+	−
Pereiopod 4 +/−	+	−	R+	R+	R+	+	+	+	+	+
Biramous +/−	−		+	+	+	+	+	+	+	−
Pereiopod 5 +/−	+	−	R+	R+	+	+	+	+	+	+
Biramous +/−	−		−	−	−	−	−	−	−	−
Abdomen										
Somite 5 – Lateral spines +/−		+	+	+	+	+	+	+	+	−
Somite 6 – Continuous with telson +/−	−	+	+	−	−	−	−	−	−	−
Pleopods +/−	+	−	−	−	−	R+	R+	R+	R+	+
Fringing setae	+/−	+				−	−	R+	R+	+
Appendix interna 2–5 +/−	+					−	−	+	+	+
Telson										
Posterior margin concave (−)/convex (+)	+	+/−	+/−	−	−	+/−	+/−	+	+	+
Spine formula	2+2	7+7	7+7	6+6	4+4	4+4	4+4	4+4	4+4	2+2
Small spines +/−	−	+	+	+	+	+	+	+	−	−
No. of pairs of lateral spines	2	0	0	0	0	0	0	0	0	2
Uropods +/−	+	−	−	+	+	+	+	+	+	+
Long plumose setae – Endopodite	31			0	9–11	14–17	17–23	30	34	37
Exopodite	37			10–12	16–19	21–25	23–30	33	35	37

[1] N.B. Many of these are estimates from poor-qgures in published work; R = rudimentary; + = present/yes; − = absent/no.

Table 2 Comparison of structure in larval development of *Palaemon (Paleander) elegans* throughout its geographical range.

| | Zoea/Moult | | |

of repeat moults in which it is reported (Rochanaburanon & Williamson, 1976) that no morphological change has occurred. This is certainly true of gross morphology but on the occasion in the present work when there was an obvious and consistent 'repeat', i.e. after zoea 6, in the subsequent intermoult individuals there were small, but significant, changes (Figs. 11b–d). The usual number of zoeae for *Palaemon* (*Paleander*) *elegans* would be six as recorded by Wimpenny & Titterington (1936), Hoglund (1943) from the plankton and by Rochanaburanon & Williamson (1976) in laboratory conditions at 20 °C. Up to nine moults may occur, however, prior to the post-larva being attained. This probably represents an adaptation to sub-optimal conditions by prolonging larval existence before metamorphosis through juvenile to adult. Although the maintenance of as near normal conditions in the laboratory is attempted, clearly the artificial system is not ideal.

Rochanaburanon & Williamson (1976) report that at 20 °C *P.* (*P.*) *elegans* goes through six and at 15° C up to nine moults before reaching first post-larva. Hoglund (1943) reported that first hatching in his Swedish samples occurred in June in 1940 when the sea temperature was 18 °C but that hatching was delayed until July in 1941 as the June temperature had reached only 16 °C. This is a likely response in the breeding behaviour of a Mediterranean species reaching the northern limits of its geographical range. This accords with the findings of Wimpenny & Titterington (1936) who record six larval stages from plankton samples taken in Lake Qarun, Egypt, collected from March to November when temperature ranged from 19 to 26·5 °C. Tsurnamal (1963), however, reported eight stages from material collected on the coast of Israel and reared in the laboratory at 25 °C. It would appear, therefore, that there are a number of environmental factors influencing the number of moults before first post-larva including laboratory 'water quality' and especially temperature. In the present study, laboratory rearing was deliberately carried out at 15 °C in order to produce a long series of larval moults before PL1 was achieved.

Several interesting features related to functional morphology have been noted in the development of *P.* (*P.*) *elegans* which will be examined closely in other British species. These features include:

1. The temporary regression of maxilliped exopodites at metamorphosis from zoea to post-larva with the changeover from thoracic to abdominal (pleopod) propulsion;
2. Feeding habits throughout larval life especially the morphogenetic changes in the mandible at the PL1 moult;
3. Swimming habits of the larvae, especially the sequence of pereiopod development and also the shape of the telson and its role as a hydrofoil as the swimming mode develops during larval life and changes fundamentally at PL1.

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Note added in Proof

For Subgenus (*Paleander*) read (*Palaeander*) throughout.

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Synopsis

The major diagnostic features of the microchiropteran family Rhinopomatidae are reviewed, with a detailed account of the sole included genus, *Rhinopoma*. Current taxonomic opinion in the genus is synthesized with the recognition and definition of three species.

Introduction

The microchiropteran family Rhinopomatidae includes but one genus, *Rhinopoma* Geoffroy, 1818, the mouse-tailed bats, widely distributed through the arid and semi-arid regions of northern Africa and southern Asia. The genus has a long taxonomic history and displays a range of variation in cranial morphology and in size that has attracted a number of names, some even as yet of uncertain application. Although small in number of species and (Koopman & Cockrum, 1967 : 117) apparently rather rare in most parts of its range, the genus nevertheless is often represented in collections, and in recent years there has been a resurgence of interest in its classification, both at the specific and subspecific levels. This review attempts to provide an interpretation of the genus as a whole, and to draw attention to its outstanding taxonomic problems.

Systematic descriptions

Family **RHINOPOMATIDAE** Dobson, 1872

Rhinopomatidae Dobson, 1872 : 221.
Rhinopomidae Miller, 1907 : 80.

Muzzle with thickened narial pad surmounted by a distinct ridge-like dermal outgrowth; tragus simple; second digit with two distinct bony phalanges; third digit with two phalanges but with no evidence of a third; tail long, mouse-like, emerging from edge of narrow uropatagium.

Skull (Fig. 1) lacking postorbital processes; lacrimal region swollen; premaxillaries separate, free, fused neither to each other nor to the adjacent parts of the skull, the narial branch well developed, the palatal branch much reduced, no more than a broadly angular thickening of the lower part of the narial branch; width of the combined nasals greater than their length; palate terminating posteriorly in the plane of the third upper molars (m^{3-3}) or just behind it; auditory bullae relatively large.

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Humerus (Fig. 2) with trochiter well developed, little smaller than the trochin, reaching to the head of the humerus or slightly exceeding it, separated from humeral head by a shallow groove, trochiter with at most only a very slight articulation with the scapula (Winge, 1923 : 267; 1941 : 310); trochin well developed, very slightly exceeding humeral head; proximal face of humerus slightly ridged; a shallow supraglenoid fossa at anterior end of groove between trochiter and head; humeral head rounded; shaft of humerus with prominent deltoid crest, not displaced; capitellum very slightly displaced from line of shaft, its principal articular surface sub-spherical; lateral surface of capitellum moderate, about one third the width of the principal surface, not extending distally as far as the principal surface; trochlea narrow, about one third or a little less than the width of the principal surface, extending distally as far; epitrochlea about one third the width of the distal articular surfaces, lacking any definite epitrochlear process or spine, its distal margin forming a slight protrusion not extending distally as far as the distal edge of the trochlea; a shallow radial fossa.

Shoulder girdle without special modification; scapula normal, acromion and coracoid processes strong, the coracoid directed laterad; supraspinous fossa a little less than one half the area of the infraspinous fossa, unridged, not angled sharply from scapular spine; infraspinous fossa moderately faceted; anterior flange of scapula moderately developed. Seventh cervical vertebra not fused with first dorsal; pelvis normal, boundaries of sacral vertebrae defined; head of femur not set at an angle to the shaft; lesser trochanter similar in size to greater trochanter but slightly lower; proximal part of femoral shaft with slight flanges; ventral surface of tibia flattened and slightly grooved posteriorly; fibula complete, thread-like for much of its length.

The family contains the single genus, *Rhinopoma*, which for the most part is distributed through the arid and semi-arid parts of southern Asia and northern Africa.

Genus ***RHINOPOMA*** Geoffroy, 1818

Rhinopoma Oken, 1816 : 926. Not available (Opinion 417, 1956).
Rhinopoma Geoffroy, 1818 : 113. *Vespertilio microphyllus* Brünnich, 1782.
Rhinopoma Bowdich, 1821 : 30. *Vespertilio microphyllus* Brünnich, 1782.
Rhinopomus Gervais, 1854 : 202 (lapsus). *Vespertilio microphyllus* Brünnich, 1782.

Sides of muzzle swollen, the lateral swellings separated above by a broad longitudinal groove, deepening posteriorly below the inner insertion of the ears; nostrils opening anteriorly in the face of a thickened, vertical narial pad, the narial openings slit-like, in the upper part of the narial pad, oblique, inclined at about 30° to the horizontal, closed in specimens preserved in alcohol; narial pad surmounted by a thickened, ridge-like transverse dermal outgrowth; lips not swollen or wrinkled; ears large, just extending beyond muzzle when laid forward, joined at inner margins by a deep integumentary band; antitragus small, poorly defined; tragus large, membranaceous and truncate, sometimes with a small swelling in its anterior margin; long, slender tail extending from edge of reduced, rather narrow uropatagium.

Skull (Fig. 1) relatively short, rather broad; lateral swellings of rostrum sometimes extending anteriorly beyond the margins of the narial aperture; narial branches of premaxillae extending upwards at sides of narial aperture; premaxillae in contact anteriorly, enclosing an anterior palatal vacuity; maxillary toothrows slightly arched; no basioccipital pits; inner margins of audital bullae flattened.

Dental formula $i\frac{1}{2}, c\frac{1}{1}, pm\frac{1}{2}, m\frac{3}{3}=28$. Upper incisor ($i^2$) minute, styliform, oblique, barely emerging from the gum, the crown scarcely differentiated from the shaft, the tips of the upper incisors only just exceeding the premaxillae; canines (c^1_1) simple, lacking distinct cingula, c^1 with anterior and posterior cutting edges. Upper premolar (pm^4) with small but obvious anterior cingulum cusp; first and second upper molars (m^{1-2}) without distinct hypocones, the protoconal and hypoconal basins broadly contiguous, especially in worn teeth; third upper molar (m^3) with metacone, mesostyle and three commissures, the third commissure very short, the mesostyle displaced inwards and the metacone small, obsolescent. Lower incisors (i_{1-2}) of equal size,

touching, tricuspid, inner and outer lobes distinct, median lobe minute, sometimes obsolete, i_2 separated from c_1 by a space about equal to one half the width of i_2; anterior lower premolar (pm_2) long, narrow, its longitudinal diameter almost twice its transverse diameter, with relatively large cusp; second lower premolar (pm_4) wider, its width about two thirds its length; third lower molar (m_3) reduced, the posterior triangle smaller than the anterior triangle, hypoconid and entoconid low but distinct.

The genus is distributed from parts of West Africa eastward at least to India, with an outlier in Sumatra; it ranges southward in Africa to northern Kenya and northwards in the Middle East to Iran. Its classification was reviewed and discussed by Thomas (1903), Wroughton (1912 : 767), Ellerman & Morrison-Scott (1951 : 101), Rosevear (1965 : 163), Kock (1969 : 27) and DeBlase, Schlitter & Neuhauser (1973): this last study provided a brief review of the taxonomic history of the genus. Currently, three species of *Rhinopoma* are recognized: two of these, *microphyllum* and *hardwickei*, are sympatric over much of the range of the genus. The third, *muscatellum*, occurs in the southern part of Iran, and in southwestern Afghanistan; at first given specific rank by Thomas, its describer, it came later to be considered a subspecies of *R. hardwickei* but is considered now to warrant recognition as a full species by DeBlase, Schlitter & Neuhauser (1973). As a general rule, the species can be distinguished locally by their relative size but criteria of size are less satisfactory when each species as a whole is compared with the others. Kock (1969 : 27) provided an exhaustive review of the African representatives of the genus; its members in the Near and Middle East were examined by Harrison (1964 : 53) and by Gaisler, Madkour & Pelikán (1972 : 7), in Afghanistan by Gaisler (1970 : 6) while Brosset (1962 : 24) studied the two species in India.

Key to the species of *Rhinopoma*

1 Larger, length of forearm 57·5–75 mm, condylobasal length 17·3–20·6 mm; tail usually shorter than forearm; prominent sagittal crest; supraorbital ridges high, knife-like, their junction enclosing a recess or pocket, angled, the frontal region more or less pentagonal in outline, flat, rostrum with narial swellings not especially pronounced . . . ***microphyllum*** (p. 31)

– Smaller, length of forearm 46–63·5 mm, condylobasal length 14·0–17·8 mm; tail usually longer than forearm; low sagittal crest; supraorbital ridges low, no prominent recess or pocket at their junction, straight, the frontal region more or less triangular, slightly depressed centrally; rostrum with prominent sub-globular narial swellings 2

2 Muzzle with well-developed transverse dermal ridge; uppermost margins of rostrum slightly divergent anteriorly; narial inflations more or less globose, not projecting laterally much beyond anteriormost point of nasals, foremost extension of swelling in profile above the rear of c^1 . . . . . ***hardwickei*** (p. 36)

– Dermal ridge on muzzle low; uppermost margins of rostrum more nearly parallel; narial inflations slightly angular, projecting considerably beyond anteriormost point of nasals, foremost extension of swelling in profile above front of c^1 . . . ***muscatellum*** (p. 40)

Rhinopoma microphyllum (Brünnich, 1782)

DISTRIBUTION. Mauritania (Poulet, 1970 : 237); Senegal (Adam & Hubert, 1972 : 62); Nigeria; Sudan; Egypt; Lebanon; Israel; Jordan; Saudi Arabia (Nader, 1975 : 334); Iran, Afghanistan; Pakistan; India; Sumatra. Earlier records of *R. microphyllum* from Mauritania and others from Morocco, Algeria and Tunisia were discussed by Kock (1969 : 41) who concluded that they referred to *R. hardwickei*. The species was reported originally from Mauritania by Dekeyser & Villiers (1952; 1956 : 44, 164, 186) and Dekeyser (1955) but the record (from Adrar) on which these reports were based is shown by Kock to be of *hardwickei*. However, Poulet (1970 : 237) records *microphyllum* and *hardwickei* sympatrically from Mauritania. The report from Morocco is based on Panouse (1951 : 38) and those from Algeria on Loche (1867 : 79); the reputed occurrence in Tunisia is doubtful (Oliver, 1909 : 148; Laurent, 1941a : 11; 1941b : 99). The genus (as *R. hardwickei*) has been reported also from Burma (Jerdon, 1867 : 29, 30) and from southern Thailand (Cantor, 1846 : 178; Jerdon, 1867 : 29, 30). Later reports (e.g. Blanford, 1891 : 362; Anderson & de Winton, 1902 : 147) evidently stem from these earlier records. Kock (1969 : 60, 62) suggested tentatively that they may refer to *R. microphyllum* but without specimens the point cannot be determined definitively.

Rhinopoma microphyllum tropicalis Kock, 1969

Rhinopoma microphyllum tropicalis Kock, 1969 : 58. Jebel Talao, 2 km NE of Kadugli, Kordofan, Sudan, 550 m.

This subspecies is distinguished by its greater size in some respects when compared with *R. m. microphyllum*, by its browner rather than greyer dorsal colour, brownish rather than whitish

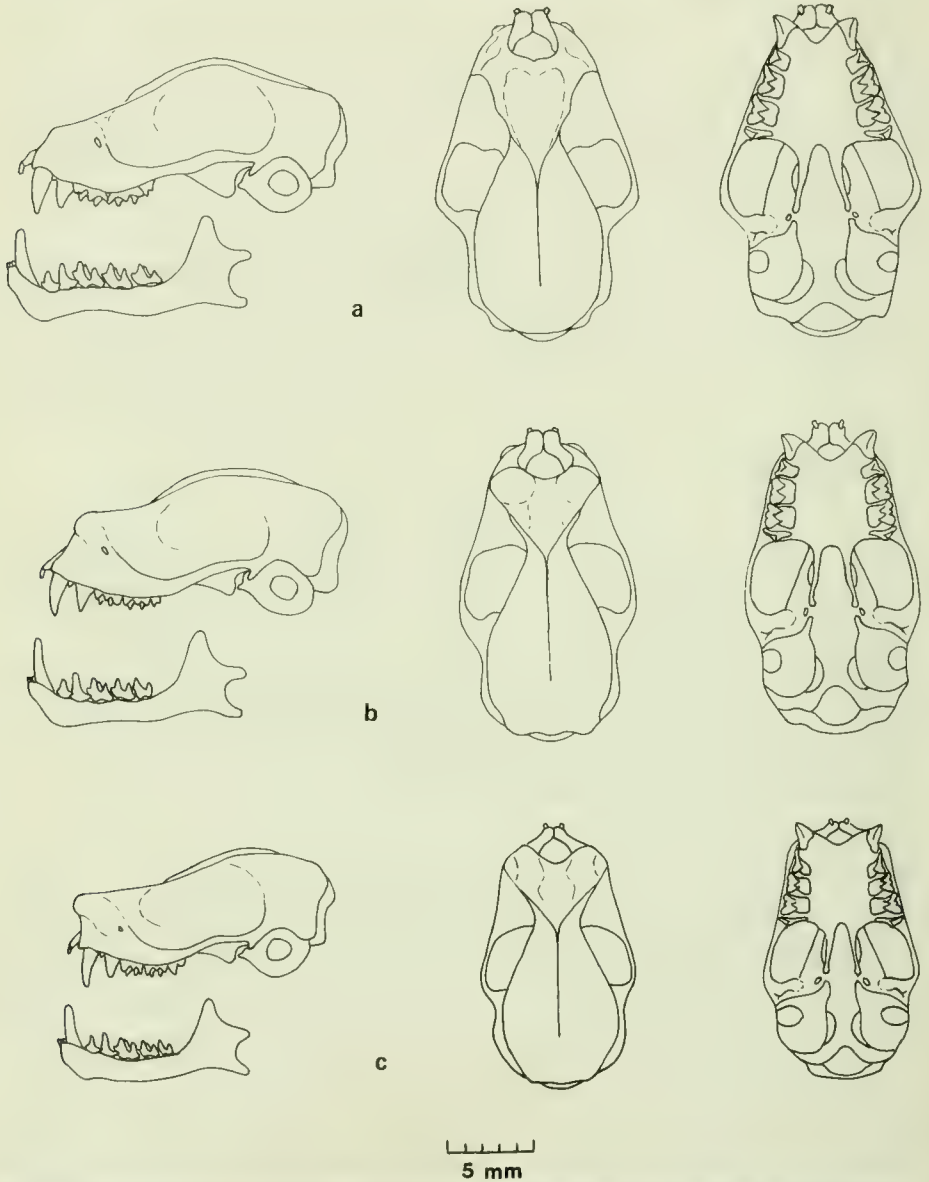

Fig. 1 Lateral, dorsal and ventral aspect of skull of (a) *Rhinopoma microphyllum microphyllum*, ♂, BM 68.485, Pakistan; (b) *Rhinopoma hardwickei arabium*, ♂, BM 13.6.19.4, Yemen; (c) *Rhinopoma muscatellum muscatellum*, ♀, BM 85.11.5.9, Muscat.

underparts, and by its broadly U-shaped rather than V-shaped mesopterygoid fossa or palation. Kock (1969 : 60, 61, fig. 6) referred all specimens from the Sudan to this subspecies, together with the large example from Wase Rock, Nigeria, recorded by Rosevear (1965 : 166). However, specimens from Jebel Auli and from Jebel Azraq, near Khartoum, in the collections of the British Museum (Natural History), are much smaller than *tropicalis* from the Nuba Mountains (Kock, 1969 : 56, tab. 9) or the example from Wase Rock. In fact, they fall within the size range of *R. m. microphyllum* and are here referred to that subspecies; Koopman (1975 : 366) also referred these and other examples from the northern Sudan to *R. m. microphyllum* (with the comment that *tropicalis* should be restricted to Kordofan, otherwise *lepsianum* Peters, 1859 whose type-locality he restricted to Khartoum probably would have to be used for it) but suggested that this area might prove to be one of intergradation.

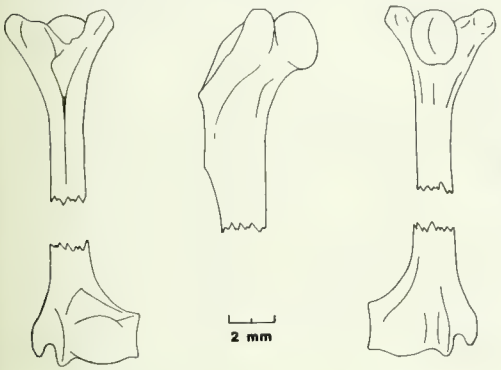

Fig. 2 Anterior, dorsal and posterior aspect of left humerus of *Rhinopoma microphyllum kinneari*, ♀ BM 62.919, India.

Rhinopoma microphyllum microphyllum (Brünnich, 1782)

Vespertilio microphyllus Brünnich, 1782 : 50, pl. 6, figs 1–4. Arabia and Egypt: according to Anderson & de Winton (1902 : 147) the original specimen came from the 'Pyramids of Gizeh'. Type-locality fixed at Giza by Koopman (1975 : 366).

Rhinopoma lepsianum Peters, 1859 : 222. Blue Nile. According to Kock (1969 : 54, 57, 58) who (p. 58) designated a lectotype, from the White Nile. This author (p. 58) thought that the original material was mislabelled and actually came from Lower Egypt. Koopman (1975 : 366) restricted the type-locality to Khartoum, and suggested that the name was based on atypical material.

(?) *Rhinopoma cordofanicum* Heuglin, 1877 : 24. Araschkol Mts (= Jebel Arashkol), Sudan. According to Koopman (1975 : 367, 434), on west side of the White Nile at *c.* 14°15′ N, 32°10′ E, Blue Nile Province.

Specimens from Mauritania and Senegal seem from their published measurements (Poulet, 1970 : 241; Adam & Hubert, 1972 : 62) to be referable to the slightly smaller subspecies *R. m. microphyllum* rather than to *R. m. tropicalis*. Otherwise the nominate subspecies is distributed from Egypt and the Sudan through much of the Near and Middle East to Pakistan. Examples from Sind (listed as *kinneari* by Wroughton, 1916 : 752), together with others from Ara in the northwestern Punjab and Amb and Rohtas in the Salt Range (Sind and Salt Range specimens are measured by Siddiqi (as Siddiqui), 1970 : 4, tab. 1, and by Gaisler, 1970 : 7, tab. 1, 8, tab. 2), are referred to *R. m. microphyllum* by Gaisler (1970 : 7). Felten (1962 : 171, 172, tab. 1) refers two specimens from Rajasthan in northwestern India to *R. m. microphyllum*: the species was first reported from Rajasthan, as *R. kinneari*, by Prakash (1961 : 445) who subsequently (Prakash, 1963 : 154, 164, tab. 2) gave further details. The measurements of the specimens examined by these authors support the view that they should be referred to *R. m. kinneari*.

Kock (1969 : 35, 40, 41, 51) considered that *cordofanicum* Heuglin, 1877 represented *R. hardwickei*, treating it as a synonym of *R. h. sennaariense* (= *R. h. arabium*, q.v.). However, Thomas (1903 : 496) noted that the German authors Peters and Heuglin, who had recognized the co-existence of a larger and a smaller form in Egypt, had been misled by the early literature and had affixed their names (*lepsianum* Peters, 1859, *cordofanicum* Heuglin, 1877) to the larger

species, already named *microphyllum* by Brünnich, 1782. Kock (1969 : 40) referred *cordofanicum* to *R. hardwickei* on account of the measurements quoted by Heuglin (1877 : 24), especially of the wing span. The forearm length of the one example cited by Heuglin is given as 2 inches 5½ lines (presumably German measure), approximately 66 mm (Kock stated 64·1 mm, the equivalent in English measure), within the range for *microphyllum*: specimens from 'Kordofan', Jebel Auli and Jebel al Azraq, all in the Sudan, in the collections of the British Museum (Natural History), range in forearm length from 62·8 to 68·8 mm. The corresponding length in *R. hardwickei* from the Sudan, from specimens in the British Museum (Natural History), is 52·8–60·4 mm. Furthermore, the collection of the British Museum (Natural History) includes an old specimen (BM 47.5.27.31, skin only), purchased of Parreys, from Arashkol. Listed by Dobson (1878 : 402), this specimen was discussed by Kock (1969 : 40) who thought that it might be a syntype of *cordofanicum*, described originally from that locality. Its forearm length of 69·7 mm, however, refers it without doubt to *R. microphyllum*, to which Koopman (1975 : 366) also allocated it. It seems likely, therefore, that *cordofanicum* represents *R. microphyllum* rather than *R. hardwickei*.

Rhinopoma microphyllum harrisoni Schlitter & DeBlase, 1974

Rhinopoma microphyllum harrisoni Schlitter & DeBlase, 1974 : 658. 10 km SE of Kazerun, Fars Province, Iran, 29°34′ N, 51°46′ E.

A small subspecies, its skull lacking well developed sagittal and lambdoidal crests and with the rostral ridges converging rather than parallel for part of their length, *R. m. harrisoni* ranges through southern Iran from Meshrageh southeastwards to 10 km WNW of Bustak.

Rhinopoma microphyllum kinneari Wroughton, 1912

Rhinopoma kinneari Wroughton, 1912 : 767. Bhuj, Cutch, India. Holotype in British Museum (Natural History).

Rhinopoma kinneri Garg, 1955 : 55. Lapsus.

This wholly Indian subspecies differs from *R. m. microphyllum* only in slightly larger average size as is demonstrated by Gaisler (1970 : 7, tab. 1, 8, tab. 2). This author gave detailed measurements of *R. m. microphyllum* from Iran (the specimen from Misham (= Mishen), Persian Gulf, is *R. m. harrisoni* according to Schlitter & DeBlase, 1974 : 662), Afghanistan and Pakistan with those of *R. m. kinneari* from a variety of Indian localities, the specimens other than those from Afghanistan being those of the collection of the British Museum (Natural History). The subspecies is distributed through central and western India: it has been reported from Rajasthan (Prakash, 1961 : 445; 1963 : 154; Felten, 1962 : 171, as *R. m. microphyllum*), Bombay, Delhi, Madhya Pradesh and Uttar Pradesh.

Ellerman & Morrison-Scott (1951 : 102) considered *kinneari* specifically distinct but subsequent authors (Aellen, 1959 : 357; Felten, 1962 : 171) have regarded it as only subspecifically separable from *microphyllum* while Siddiqi (1961 : 106; 1970 : 4 (the latter as Siddiqui)) synonymized it with *microphyllum*. Kock (1969 : 60) thought that *kinneari* might be a possible synonym either of *microphyllum* or of *sumatrae*.

Rhinopoma microphyllum sumatrae Thomas, 1903

Rhinopoma sumatrae Thomas, 1903 : 497. Balighe, near Lake Toba, north Sumatra. Holotype in British Museum (Natural History).

Few specimens of this subspecies are known and these differ but little from *kinneari*; Thomas diagnosed it on grounds of great size but their dimensions in fact fall within the range of those of the Indian subspecies. The remark by its describer that *sumatrae* differs from the Indian *R. hardwickei* not only in size but in the non-inflation of its nasal prominences confirms its allocation to *R. microphyllum*, and Kock (1969 : 59, 60) considered that *kinneari* might be a possible synonym of *sumatrae*. To synonymize these at present introduces a widely discontinuous distribution since *sumatrae* has been reported only from the type-locality; it should be noted that it is the prior name.

Table 1 Measurements (in millimetres) of *Rhinopoma microphyllum*.

	Length of forearm		Condylobasal length		Condylocanine length		Zygomatic width		Mastoid width		c–m³	
	n	R	n	R	n	R	n	R	n	R	n	R
R. m. tropicalis												
Nigeria[1]	1	74·9	1	20·6	1	20·0	1	13·5	1	10·9	1	7·7
Sudan (Nuba Mts)[2]	6	70·2–74·0	6	19·4–20·1			6	12·6–13·1			6	7·2–7·5
R. m. microphyllum												
Mauritania[3]		61–68										
Senegal[4]	1	66	1	20·2			1	11·5			1	7·2
Sudan (Khartoum)[1] *	5	62·8–68·8	1	18·1	2	17·6–18·1	2	11·8	2	9·5–9·7	2	6·8–7·2
Sudan (Arashkol)[1]	1	69·7										
Egypt[1]	4	59·9–69·3	2	18·0–18·8	2	17·7–18·5	1	11·8	2	9·7–9·9	2	7·2–7·4
Lebanon, Israel[5]	3	68·2–71·7	2	19·6–20·2			1	12·7–12·8			2	8·2
Jordan[1]	1	64·2	1	19·1	1	18·6		–	1	9·6	1	7·2
Saudi Arabia[6]	1	69	1	19·5			1	12·3			1	7·2
Iran[1, 7]	12	65·3–70·1	11	18·8–20·0	1	18·4	13	12·0–13·1	1	9·9	13	6·7–7·6
Afghanistan[8, 9]	93	62·0–70·5	77	18·0–20·1	2	18·7–19·3	85	11·1–12·8	79	9·2–10·2	91	7·0–7·8
Pakistan[1]	17	62·9–71·5	11	17·6–19·2	14	17·2–19·0	9	11·4–12·4	13	9·3–10·3	16	6·8–7·3
R. m. harrisoni												
S. Iran[1, 6]	26	57·5–66·1	27	17·3–19·5	1	18·5	27	10·8–12·4		–	10	6·4–7·3
R. m. kinneari												
India[1]	12	66·0–73·6	12	19·5–20·5	12	18·8–19·9	11	12·2–13·4	12	10·4–11·1	12	7·3–7·9
Rajasthan, India[10]	2	70					2	12·5			2	7·3–7·6
Rajasthan, India[11]	84	64·5–75·0	12	20·0–21·2			12	12·0–13·5				
R. m. sumatrae												
Sumatra[1]	2	68·8–70·6	2	19·4–20·0	2	18·9–19·7	2	12·5–12·7	2	10·2–10·4	2	7·5–7·8

n = number of specimens; R = range.

* The type-locality of *lepsianum* Peters, 1859 is restricted to Khartoum by Koopman (1975 : 366). A lectotype and paratype from 'White Nile' designated by Kock (1969 : 58) measure (p. 56, tab. 9): length of forearm (1) 68·9, condylobasal length (2) 19·0–19·7, zygomatic width (2) 13·1, mastoid width (2) 10·0–10·7, c–m³ 6·8–7·2.

[1] British Museum (Natural History); [2] Kock, 1969 : 56, tab. 9; [3] Poulet, 1970 : 241; [4] Adam & Hubert, 1972 : 62; [5] Harrison, 1964 : 55, tabs 25, 26; [6] Nader, 1975 : 334; [7] Schlitter & DeBlase, 1974 : 660, tab. 1; [8] Aellen, 1959 : 358, 359; [9] Gaisler, 1970 : 7, tab. 1, 8, tab. 2; [10] Felten, 1962 : 172, tab. 1; [11] Prakash, 1963 : 164, tab. 2.

DISTRIBUTION. Niger; Mauritania; Morocco; Algeria; Tunisia; Egypt; Sudan; northwestern Kenya; Ethiopia; French Somaliland (Territory Afars & Issas); Somalia; Socotra I.; Israel; Jordan; Saudi Arabia; Aden; Yemen; South Yemen; Muscat and Oman; Iraq; Iran; Afghanistan; Pakistan; India; reported from Burma (Jerdon, 1867 : 29, 30) and from southern Thailand (Cantor, 1846 : 178) but this latter record listed as *R. microphyllum* by Kloss (1908 : 155). It is not clear whether these reports from Burma and Thailand refer to *R. hardwickei* or to *R. microphyllum*; Kock (1969 : 62) tentatively allocates the records that stem from them (i.e. Blanford, 1891 : 253; Anderson & de Winton, 1902 : 147; Chasen, 1940 : 31; Ellerman & Morrison-Scott, 1951 : 102) to *microphyllum*.

There is a widespread local size variation in *R. hardwickei* leading to the recognition of a number of subspecies; until recently it has been customary for authors to refer the greater part of the African population to *R. h. cystops* Thomas, 1903, on occasion including with it the population in the Near East sometimes referred to *R. h. arabium* Thomas, 1913. A small subspecies, *R. h. macinnesi* Hayman, 1937 has been recognized in northern Kenya and the southern Sudan although Hayman & Hill (1971 : 14) thought it a probable synonym of *cystops*; further small forms, *R. h. muscatellum* Thomas, 1903, *R. h. seianum* Thomas, 1913 and *R. h. pusillum* Thomas, 1920 have been reported from Oman and southern Iran, while the nominate subspecies has been restricted to Afghanistan, Pakistan and India. The species was reviewed in considerable detail by Kock (1969) who recognized six subspecies.

DeBlase, Schlitter & Neuhauser (1973), however, have raised *muscatellum*, with synonym *pusillum* and valid subspecies *seianum* to the rank of a full species, and Kock (1969) and Gaisler, Madkour & Pelikán (1972) have suggested that the pattern of subspeciation may be more complicated than originally thought. Kock (1969 : 35, 42, map, 51), in a detailed review, recognized a smaller, central Saharan subspecies, *R. h. cystops*, extending from Hoggar in Algeria and Air in Niger to central Egypt, surrounded by a larger subspecies, *R. h. sennaariense* Fitzinger, 1866, which extends also into the Near East and Arabia, with a smaller subspecies, *R. h. macinnesi*, extending from the southeastern Sudan and northern Kenya to Somalia and to Assab in Eritrea, Ethiopia. This author considered the Arabian form *R. h. arabium* a synonym of *R. h. sennaariense* and allocated eastern Arabian and Iranian specimens to *R. h. muscatellum* (including *pusillum*) and *R. h. seianum*, with the nominate subspecies in Afghanistan, Pakistan and India. Koopman (1975 : 367) agreed with Kock for the African representatives of the species, but pointed out that *sennaariense* is a nomen nudum and in its place used *cordofanicum* Heuglin, 1877. This author also recorded four specimens from French Somaliland (Territory Afars & Issas) which agree well with the larger of the African subspecies rather than with the smaller *R. h. macinnesi*.

In a study of the Egyptian population, Gaisler, Madkour & Pelikán (1972 : 7) adopted the views of Kock for the African and Near East populations but from an examination (p. 8, fig. 1) of the condylobasal length and toothrow length of specimens from these areas gave an indication of the variability of the two parameters. They concluded that this analysis confirmed that the specimens from the Upper Egyptian population are smaller in these respects than those from the population in Lower Egypt; that specimens from the Near East have a relatively short upper toothrow, with the lowest values in the Yemen; and that the Sudanese population is intermediate between those from Lower Egypt and the Near East. These authors suggested that the analysis indicated that the matter can be resolved in various ways: (1) by recognizing but a single subspecies; (2) by separating the Upper Egyptian population and classifying those remaining as a single subspecies; or (3) by recognizing the Sudanese population, the Upper Egyptian population and the Arabian population as distinct subspecies, and describing the population in Lower Egypt as new. It is clear from the data assembled by Gaisler, Madkour & Pelikán that the variation is largely clinal, but erratic; the variations in size may reflect the vagaries of climate as is suggested by Kock (1969 : 48, 50, tab. 8).

The view adopted here is that of Kock (1969); *cystops* is retained for a smaller, Saharan subspecies, surrounded in Africa by a slightly larger form which Kock calls *sennaariense*, with a yet smaller form, *macinnesi*, in the southeastern Sudan, northeastern Kenya and perhaps in Somalia and eastern Ethiopia. Specimens from Israel, Jordan, Arabia and from the remainder of the

Near and Middle East are referred to the larger of the African forms, while those from Afghanistan, Pakistan and India are considered to represent the nominate subspecies and are yet rather larger. The small size variations noted by Gaisler, Madkour & Pelikán seem scarcely to justify further subspecific recognition, and, indeed, may become less significant when collections become more representative.

Rhinopoma hardwickei cystops Thomas, 1903

Rhinopoma cystops Thomas, 1903 : 496. Luxor, Egypt. Holotype in British Museum (Natural History).

Kock (1969 : 52) referred specimens from Algeria (Hoggar), Niger (Air) and from central and Upper Egypt to *R. h. cystops*. These average a little smaller than other populations of *R. hardwickei* from northern Africa.

Rhinopoma hardwickei arabium Thomas, 1913

Rhinopoma sennaariense Fitzinger, 1866 : 547. Sennaar and Fazuglo (= Fazughli), near Roseires, Sudan. Type-locality restricted to Fazughli by Kock (1969 : 35). Nomen nudum.
Rhinopoma longicaudatum Fitzinger, 1866 : 547. Sennaar, Sudan. Nomen nudum.
Rhinopoma senaarense, potius *senarense* Heuglin, 1877 : 24. Emendation of *sennaariense* Fitzinger, 1866.
Rhinopoma cystops arabium Thomas, 1913 : 89. Wasil, Yemen, 4000 ft [1200 m]. Holotype in British Museum (Natural History).
Rhinopoma arabicum K[innear], 1916 : 3. Mesopotamia (= Iraq). Lapsus.
Vespertilio ferox Stresemann, 1954 : 172. Sackhara (= Saqqara), Egypt. Label name ex Hemprich, without nomenclatorial status.
Vespertilio brevicauda Stresemann, 1954 : 172. Sackhara (= Saqqara), Egypt. Label name ex Hemprich, without nomenclatorial status.
Rhinopoma lardwickei cystops Madkour, 1961 : 50. Lapsus.
Rhinopoma hardwickei sennaariense Kock, 1969 : 40, 51. Fazogli (= Fazughli), Blue Nile, Sudan. Validation ex Fitzinger, 1866, nomen nudum.
Rhinopoma senaariense Koopman, 1975 : 367. Lapsus.

This subspecies, very slightly larger on the average than *R. h. cystops*, is distributed through Mauritania, Morocco, Algeria, Tunisia, Niger, Sudan, Lower Egypt, Ethiopia and French Somaliland (Territory Afars & Issas); it extends to the island of Socotra and to Israel, Jordan and Arabia, eastward to Iran.

Kock (1969 : 40, 51) employed *sennaariense* Fitzinger, 1866, for this subspecies but the account by Fitzinger (1866 : 547) provides no descriptive information at all, consisting merely of the name and locality. Neither is the name validated by Heuglin (1877 : 24), who emended it but provided no descriptive material. According to Gaisler, Madkour & Pelikán (1972 : 7), the discovery of the type-specimen in the Vienna Museum by Kock supports the validity of the name but in fact this discovery has no bearing on its nomenclatorial status. The first use of *sennaariense* with any descriptive data appears to be that of Kock (1969); in these circumstances the first available name, *arabium* Thomas, 1913, is used for the subspecies. Koopman (1975 : 367) pointed out that *sennaariense* Fitzinger, 1866 is a nomen nudum and used *cordofanicum* Heuglin, 1877 for the larger of the African subspecies. But this name (see above, p. 33) is likely to be a synonym of *R. microphyllum*.

Rhinopoma hardwickei macinnesi Hayman, 1937

Rhinopoma cystops macinnesi Hayman, 1937 : 530. Bat Island, near Central Island, Lake Rudolf, Kenya. Holotype in British Museum (Natural History).

A very small subspecies, reported from the southeastern Sudan by Kock (1969 : 42, fig. 5, 52) and by Koopman (1975 : 368) and from Ethiopia (Assab, Eritrea) and Somalia (Bender Cassim) by the former author (1969 : 42, fig. 5, 52), but originally described from Lake Rudolf in northeastern Kenya and in that country reported from Lake Baringo by Kock (1969 : 42, fig. 5, 45, tab. 6, 52). Elsewhere, Kock (1969 : 50, tab. 8) lists Sudanese and Kenyan specimens as *macinnesi* but those from Assab, Eritrea and Bender Cassim, Somalia, as *cystops*. Largen, Kock & Yalden

Table 2 Measurements (in millimetres) of *Rhinopoma hardwickei*.

	Length of forearm		Condylobasal length		Condylocanine length		Zygomatic width		Mastoid width		c–m³	
	n	R	n	R	n	R	n	R	n	R	n	R
R. h. cystops												
Niger (Air)[1, 2]	2	52–55·5	1	15·6	1	15·0	1	9·4	1	8·5	2	5·2–5·3
Algeria[2]		–		–			1	9·9			1	6·0
Central and Upper Egypt[1, 3, 4]	55	46·2–57·0	31	14·9–16·2	3	14·9–15·0	32	9·5–10·2	25	8·0–8·9	32	5·4–6·0
R. h. arabium												
Niger (Zinder)[2]	15	54–61·5	8	16·2–16·7			8	9·8–10·3			8	5·7–6·1
Mauritania[5]		52–58										
Morocco[2]	? 1	59										
Tunisia[2]	? 1	56	? 1	16·7			? 1	10·3			? 1	6·3
Lower Egypt[1, 3, 4]	69	50·3–62·0	46	15·3–16·9	1	15·5	42	9·6–11·0	38	8·3–9·3	51	5·6–6·5
Sudan[1, 2, 6]	116	52·0–62·1	30	15·0–17·1	47	14·4–16·5	26	9·6–11·8	3	8·2–8·7	82	5·0–6·1
Ethiopia[1]	14	52·9–56·6	7	15·0–15·7	7	14·4–15·4	3	9·4–9·9	7	8·0–8·9	7	5·5–5·7
French Somaliland	4	56–59			3	15·2–16·0						
Socotra I.[1, 7]	55	51·5–61·5	15	15·5–16·8			16	9·8–10·6			17	6·0–6·4
Israel[8]	31	50·6–59·3	29	15·5–17·2			23	9·6–10·6			29	5·3–6·1
Jordan[1, 8]	5	54·8–57·3	5	15·8–16·6	3	15·5–16·1	5	10·0–10·3	3	8·6–8·9	5	5·7–6·6
Saudi Arabia[1]	17	52·1–57·8	5	15·4–15·3	7	15·2–16·0	4	9·8–10·3	7	8·3–9·2	5	5·6–6·0
Aden; Sira I.; Jazirat-el-Abid (Slave I.)[1, 9]	17	49·3–57·9	5	15·2–16·1	3	15·0–15·8	5	8·8–15·8	3	8·4–8·7	7	5·2–5·9
Yemen[1]	8	53·5–57·5	7	15·0–16·4	7	14·9–16·3	8	9·7–10·2	10	8·5–9·6	7	5·6–6·0
Iran[10]	12	52·4–60·0	6	15·6–16·9			5	9·6–10·9			9	5·7–6·3
R. h. macinnesi												
Kenya[1]	12	45·6–50·6	2	14·0–14·1	2	13·7	2	8·4–8·6	2	7·8	2	5·1
SE Sudan[6, 7]	2	48–48·4	1	15·5	1	14·6	1	9·6			2	5·6
Ethiopia (Assab)[7, *]	? 1	47·2	? 1	14·6			? 1	9·2			? 1	5·6
Somalia (Carim)[7, †]	? 1	50·5	? 1	14·1			? 1	9·9			? 1	6·0
Somalia (Carim)[11, †]	2	50–51			2	14·7–15·0						

(Table 2 cont.)

R. h. hardwickei												
Afghanistan[12]	17	56·0–63·5	17	16·2–17·4			17	10·0–11·1	17	8·3–9·4	17	6·0–6·4
Pakistan[1]	10	57·7–63·1	8	15·9–17·5	10	15·5–17·0	6	10·0–10·7	10	8·6–9·4	10	5·9–6·3
India[1]	40	53·3–62·7	19	16·3–17·8	30	15·7–17·5	23	10·3–11·6	30	8·7–9·8	32	5·8–6·8

n = number of specimens; R = range.
* Referred to *R. muscatellum* by Largen, Kock & Yalden, 1974 : 230.
† Probably based on same material.
[1] British Museum (Natural History); [2] Kock, 1969 : 39, tab. 5; [3] Kock, 1969 : 38, tab. 4; [4] Gaisler, Madkour & Pelikán, 1972 : 9, tab. 3, 10, tab. 4; [5] Poulet, 1970 : 241; [6] Koopman, 1975 : 367; [7] Kock, 1969 : 45, tab. 6; [8] Harrison, 1964 : 57, tab. 27, 59, tab. 28; [9] Harrison, 1964 : 58, tab. 27, 60, tab. 28; [10] DeBlase, Schlitter & Neuhauser, 1973 : 837, tab. 2; [11] Koopman, 1975 : 368; [12] Gaisler, 1970 : 9, tab. 3, 10, tab. 4.

Table 3 Measurements (in millimetres) of *Rhinopoma muscatellum*.

	Length of forearm		Condylobasal length		Condylocanine length		Zygomatic width		Mastoid width		c–m³	
	n	R	n	R	n	R	n	R	n	R	n	R
R. m. muscatellum												
Oman; Iran[1, 2]	27	45·0–52·4	12	14·2–15·5	5	13·7–14·6	12	8·9–9·5	4	8·0–8·2	14	5·2–6·1
R. m. seianum												
E Iran; Afghanistan[1, 3, 4]	13	51·5–54·8	12	15·0–16·2	4	14·8–15·5	11	9·4–10·1	4	8·0–8·4	4	5·8–6·1

n = number of specimens; R = range.
[1] British Museum (Natural History); [2] DeBlase, Schlitter & Neuhauser, 1973 : 837, tab. 2; [3] Zimmerman, 1956 : 196; [4] Aellen, 1959 : 356, 357.

(1974 : 230) refer the two very small specimens from Assab (first reported by Senna, 1905 : 292, later referred to *macinnesi* by Kock, 1969 : 42, fig. 5, 52, or listed as *cystops* by the same author, 1969 : 50, tab. 8) to *muscatellum* but did not examine them. They say, 'Senna's (1905) specimens have not been re-examined but are presumed to belong here'. According to Koopman (1975 : 368), specimens from Carim, Somalia (two females, in the Museo Civico di Storia Naturale 'Giacomo Doria', Genoa), are larger than *macinnesi*, with length of forearm 50–51 mm and condylocanine length 14·7–15·0 mm. This author also recorded four specimens from Ali Sabiet, French Somaliland (Territory Afars & Issas), with length of forearm 56–59 mm, condylocanine length in one male 16·0 mm, in two females 15·2–15·5 mm. These agree more nearly with *R. h. arabium*. Comparative measurements given by Kock (1969 : 45, tab. 6) include one of the specimens from Assab.

Rhinopoma hardwickei hardwickei Gray, 1831

Rhinopoma hardwickei Gray, 1831 : 37. India. Holotype in British Museum (Natural History).

The largest of the subspecies of *R. hardwickei*, the nominate subspecies occurs in eastern Afghanistan, in Pakistan and in India. Records of *Rhinopoma* from Burma and from southern Thailand are problematical, as already noted (pp. 31, 36). This subspecies has been reported as far north as the environs of Jalalabad in Afghanistan, in the Salt Range in the north of Pakistan and in India as far east as Bihar. It has not been reported from Sri Lanka, but in India specimens have been obtained as far south as the Palni Hills, Madras, 10°14′ N, 77°33′E.

Rhinopoma muscatellum Thomas, 1903

DISTRIBUTION. Oman; southwestern, southern and eastern Iran; southern Afghanistan; (?) Ethiopia (Eritrea).

For many years *R. muscatellum* Thomas, 1903, *R. muscatellum seianum* Thomas, 1913 and *R. pusillum* Thomas, 1920 were considered to be subspecies of *R. hardwickei*. However, DeBlase, Schlitter & Neuhauser (1973) have demonstrated that these small forms of *Rhinopoma* differ in one external and four cranial features from *hardwickei*, and, furthermore, that *muscatellum* and *hardwickei* occur sympatrically in southern Iran.

Rhinopoma muscatellum differs from *R. hardwickei* in the shape of the superior transverse dermal ridge surmounting the narial pad; in *R. hardwickei* this ridge is quite well developed and may be evenly rounded or have a small medial dorsal papilla but in *muscatellum* the noseleaf is at most poorly developed and consists only of a low ridge that may be flat above or may have a slight medial depression. Cranial differences on the whole are more definite; in *muscatellum* the upper parts of the rostrum are not greatly divergent; the narial inflations are relatively larger and slightly angular, projecting considerably beyond the anteriormost point of the nasals, with their foremost extension lying above the front of the canine (c^1); the palation is generally V-shaped and as a rule terminates beyond the plane of the last molars (m^3 ^{3}); the post-palatal projection is narrower (least breadth 1·6–2·2 mm as against 2·2–2·7 mm in *hardwickei*); and although there is some overlap in size, *muscatellum* is generally smaller than the Asiatic subspecies of *hardwickei*. In this latter species the uppermost margins of the rostrum tend to be divergent; the narial inflations are globose and do not extend anteriorly to any great extent, not extending greatly beyond the anteriormost point of the nasals and with their anteriormost point lying above the rear of c^1; the palation is generally U-shaped and as a rule terminates in the plane of the last molars, and the post-palatal extension is wider even in the very small subspecies *macinnesi* from the Sudan and Kenya.

Rhinopoma muscatellum muscatellum Thomas, 1903

Rhinopoma muscatellum Thomas, 1903 : 498. Wadi Bani Ruha, Muscat, Oman. Holotype in British Museum (Natural History).

Rhinopoma pusillum Thomas, 1920 : 25. Sib, southeastern Iran. Holotype in British Museum (Natural History).

The subspecies ranges from Oman and southwestern Iran eastwards almost to the Iran–Pakistan border, in Baluchistan. Largen, Kock & Yalden (1974 : 230) refer two small specimens of *Rhino-*

poma from Assab, Eritrea, Ethiopia to *R. muscatellum*, without direct examination. These hitherto have been allocated to *R. hardwickei* and are discussed under that species (p. 37); if correctly they represent *R. muscatellum* they are the first of the species to be reported from Africa.

Lay (1967 : 133) concluded from an examination of a series of specimens that *pusillum* Thomas, 1920, originally distinguished from *seianum* Thomas, 1913 on the grounds of small size, much smaller teeth and shorter tail, fitted into the range of size variation observed among topotypical material of *seianum* with which he compared it, and consequently synonymized *pusillum* with *R. hardwickei seianum* (= *R. muscatellum seianum*). However, DeBlase, Schlitter & Neuhauser (1973 : 838) refer specimens from southeastern Iran, including *pusillum*, to *R. muscatellum muscatellum*.

Rhinopoma muscatellum seianum Thomas, 1913

Rhinopoma muscatellum seianum Thomas, 1913 : 90. Seistan, Iran. Holotype in British Museum (Natural History).

Distinguished from *R. m. muscatellum* by generally larger size and proportionately smaller bullae, and reported from eastern Iran, near the border with Afghanistan, and from southern Afghanistan.

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The Stalk-joints of Recent Isocrinidae (Crinoidea) Michel Roux

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The stalk joints of recent Isocrinidae (Crinoidea)

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Synopsis

The stalk joints of recent genera representative of the crinoid family Isocrinidae have been observed with the scanning electron microscope. This study indicates that the detailed morphology of the symplexial and synostosial articulations has taxonomic significance. *Neocrinus* and *Hypalocrinus* differ from the other genera by many characters. They have affinities with the fossil *Balanocrinus* group. Such a study is of interest for comparison between the fossil and recent taxa with respect to the variability of the external morphology of the stalk.

Introduction

Many fossil species of stalked crinoids have been described from dissociated parts of their columns, their calyces and arms being unknown. When a primarily fossil family includes recent representatives, it is very important for palaeontological studies to have detailed descriptions of the stalk joints of the modern species. With this in mind I have observed columnal facets of recent Isocrinidae under the scanning electron microscope. An earlier study (Roux, 1974) suggested that the microstructural organization of the pentalobate stalk joints has taxonomic significance. To confirm this possibility, I have selected mature columnals of all the recent genera and of four species of the genus *Metacrinus*. The following Isocrinidae are described:

Metacrinus nobilis Carpenter
M. rotundus Carpenter
M. angulatus Carpenter
M. wyvillei Carpenter
Cenocrinus asterius (Linnaeus)
Endoxocrinus parrae (Gervais)
Teliocrinus springeri (Clark)
Diplocrinus alternicirrus (Carpenter)
Annacrinus wyvillethomsoni (Jeffreys *in* Wyville Thomson)
Neocrinus blakei (Carpenter)
N. decorus (Wyville Thomson)
Hypalocrinus naresianus (Carpenter)

All the specimens used belong to the zoological collections of the British Museum (Natural History), except for that of *Annacrinus wyvillethomsoni*, which is from the Muséum National d'Histoire Naturelle, Paris.

Main morphological features of stalk joints

The heteromorphic column of the isocrinids is composed of varying numbers of internodal

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columnals between single larger columnals differentiated as nodals and bearing cirri. The joint between two successive internodals is usually a symplexy; that is it has interlocking radiating ridges (culmina) and grooves (crenellae), each matching culmen and crenella making a crenula, the crenulae of each joint together making a crenularium. The distal joint of each mature nodal is a synostosis, having facets with smooth surfaces. These are the two main kinds of articulation in the columnals of this family. I have never observed syzygial articulations (in which the ridges of the crenularium correspond to elevations of the apposed facet). The term syzygy has been misapplied by many previous authors to the distal articulations of the nodals. Some symplexial or synostosial articulations have one facet with a concave surface corresponding to a convexity of the opposing facet, especially in synostoses where the distal facet of the nodal is often concave; such a modified joint is a symmorphy. The terminology used here for the morphology of stalk joints mainly follows that of Moore *et al.* (1968 : 14–16).

The microstructure of the endoskeleton is very important for a detailed description (Roux, 1970, 1974, 1975; Macurda & Meyer, 1975). The mesoderm secretes a mesh-like stereom with either a regular organization of parallel galleries (α-stereom) or a variable irregular one (β-stereom). The spiculate origin of this meshwork of calcite is evident during growth (Fig. 3A); exceptionally spicules become visible within the occluded axial canal of a synostosis (Fig. 8A, C, E).

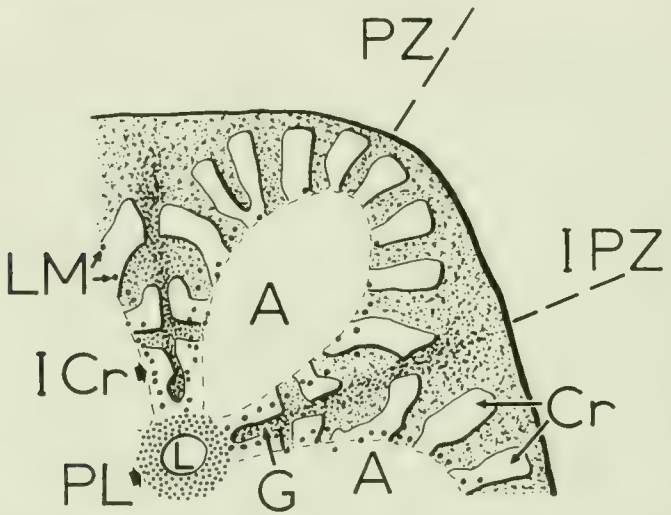

Fig. 1 Morphology of a stem joint of an isocrinid. A: areola, Cr: crenulae, ICr: inner crenularium, IPZ: interpetaloid zone, PZ: petaloid zone, G: axial groove, L: lumen, LM: large meshes, PL: perilumen.

Symplexial articulations have a pentalobate crenularium around five petaloid areolae (petaloid zones or petals).

The α-stereom is the microstructure of petaloid zones and the β-stereom of interpetaloid zones. The areola has a lanceolate or triangular shape. It may reach the outer edge of the facet (in an open crenularium, Fig. 2A) or may not (closed crenularium, Fig. 2B). A transverse section of a facet clearly shows the microstructural organization of the columnal (Fig. 2). The α-stereom of the areola takes various forms, a thin calcite meshwork with diamond-shaped meshes (Fig. 3D), or with polygonal or round meshes (Fig. 3E, F). Each end of the crenularium is formed of α-stereom with a few wider meshes. Such meshes are always visible on facets (of symplexies or synostoses) and in transverse sections; sometimes they are evenly distributed around the areola. The areolae of the fossil isocrinid *Isselicrinus subbasaltiformis* possess many such meshes (Fig. 3C) but I have

never found this texture in the areolae of the recent species described here. The inner part of the symplexial crenularium is frequently differentiated, when its surface is flatter with a thickened stereom (Fig. 4B). The axis of an interpetaloid zone often appears as a line where crenulae adjoin (Fig. 5B), or as a β-stereom groove (Fig. 5A). When the perilumen is clearly differentiated it consists of a massive covering of calcite (Fig. 5E) or sometimes of a granulose surface with little meshes (Fig. 4F).

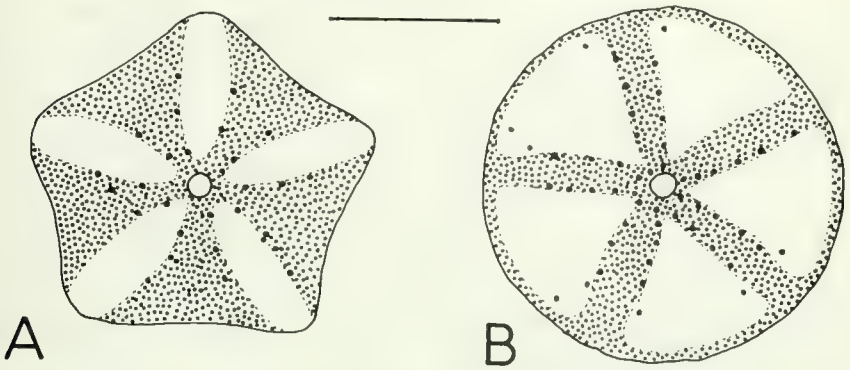

Fig. 2 Microstructural organization of a columnal in transverse section. (A) *Diplocrinus alternicirrus*; (B) *Hypalocrinus naresianus*. (Scale: 2 mm)

Synostosial articulations are secondarily ankylosed joints derived from a primary symplexial pattern in the proximal part of the column (Roux, 1974). A special stereom (synostosial stereom) with small meshes fills up the interarticular space (Fig. 3B). The greater part of the whole facet is overgrown with this stereom. The reduced crenularium has two forms: the first one (Fig. 7A) with a true synostosial stereom, the other one (Fig. 7B) with a thicker calcite stereom (like the syzygial stereom). Sometimes a radial groove (Fig. 7D) or simply a microstructural differentiation along a radial line (Fig. 7E) marks the interpetaloid axes. Applying the terminology of Moore *et al.* (1968), such a synostosis is often not a true zygosynostosis but corresponds with a crypto-symplexial pattern. Into the axial canal grows a secondary β-stereom with large meshes (axial synostosial stereom) of varying development (Fig. 8). Sometimes it fills the whole lumen; the new lumen is then often pentalobate and the axes of the petals are the interpetaloid axes of the facet. The complex axial canal of Palaeozoic crinoid columnals is probably not homologous with the occluded axial canal in isocrinid synostoses. Consequently, a few of the morphological terms of Moore *et al.* (1968) are not used here (e.g. jugulum, spatium, claustrum).

In the present paper I have not dealt with the biometry and growth of the stereom of each species but have simply described the detailed morphology of mature stem joints. However, it is important to bear in mind the ontogenetic evolution during growth of the column from the calyx to the distal part of the stalk. My purpose here is an initial comparison between the main features of the stalk joints of different taxa of isocrinids, to show their taxonomic significance.

Taxonomic significance of Isocrinid stalk joints

According to A. H. Clark (1923), the recent genera of this family are primarily distinguished by characters derived from the post-radial division series (Table 1). However, he used characters of the stalk to differentiate between the two genera *Diplocrinus* and *Annacrinus*. Although Clark thought that no fossil species are congeneric with recent ones, Rasmussen (1961) refers several Cretaceous species to recent genera. Notably he regards *Neocrinus blakei* as a recent representative of the fossil genus *Isocrinus* but in my opinion there is insufficient proof of this relationship

Table 1 Recent genera of Isocrinidae (after Clark, 1923).

Genus	I Br 2	II Br and following division series	Geographical range
Metacrinus (including *Saracrinus*)	not axillary	variable; often more than 6 elements	E. and S.E. Pacific Ocean
Cenocrinus	axillary	variable; outer series of more than 6 elements	Atlantic Ocean (West Indies)
Teliocrinus	axillary	variable; never more than 4 elements	Indian Ocean
Endoxocrinus	axillary	1+2 3 ax	Atlantic Ocean (West Indies)
Diplocrinus	axillary	1+2 ax	W. Atlantic Ocean; E. Pacific Ocean
Annacrinus	axillary	1+2 ax	N.E. Atlantic Ocean
Neocrinus	axillary	often of 4 elements or more than 4 elements	W. Atlantic Ocean
Hypalocrinus	axillary	[10 arms only]	E. Pacific Ocean

and further comparison of all possible arm and stalk characters is needed. In the present paper, Clark's definitions of genera are used, with the exception of *Saracrinus*, which was referred to the synonymy of *Metacrinus* by Gislén (1927).

The taxonomic significance of the characters provided by stalk joints is evident if we compare the division series of the arms of different genera. Several aspects of the morphology of symplexial facets make it possible to recognize different taxonomic levels of affinity (Table 2). These agree with the relationships between genera derived from Clark's (1923) key. This is not clear for synostosial characters (Table 3), the taxonomic weight of which is more often at the specific level. This is a consequence of the secondary modification of stalk joints from symplexies to synostoses. In the four species of the genus *Metacrinus* observed here, the facets of the symplexial joints appear rather different at first glance, in spite of all the main characteristic textures which they have in common. The apparent generic significance of differences in synostosial morphology found in *Cenocrinus*, for instance, is probably due to our insufficient knowledge of such monotypic genera.

An analysis of common characters (Table 4) including all the main aspects of arm division, symplexy and synostosis highlights several points concerning the affinities of the species studied here:

(1) In 31 cases, the number of common characters between two genera is less than five. The most important contrast is between *Neocrinus–Hypalocrinus* and the remaining genera (26/31 cases) and the second is between *Diplocrinus–Annacrinus* and *Metacrinus*. *Neocrinus* and *Hypalocrinus* both have stalks with strong affinities with the fossil *Balanocrinus*-group (see Roux, 1970), especially *Hypalocrinus*. During mesozoic times the stalk joints of crinoids having affinity with *Isocrinus* and those affiliated with *Balanocrinus* were very different. This observation reinforces my doubts about Rasmussen's view (1961) that *Neocrinus blakei* is congeneric with fossil species of *Isocrinus*. However, it *is* likely that *Neocrinus blakei* and *N. decorus*, the type-species of *Neocrinus*, belong to distinct genera since they have only four symplexial characters in common. A detailed study of the crowns of these species is necessary to solve this problem.

(2) The two main groups of modern Isocrinidae seem to possess two opposite patterns of symplexial joints, for instance *Metacrinus* and *Diplocrinus* on the one hand, as opposed to *Neocrinus blakei* and *Hypalocrinus naresianus* on the other.

(3) The genus *Metacrinus* is particularly well defined. *M. nobilis* and *M. rotundus* have the strongest affinities, while *M. wyvillei* is slightly different from *M. nobilis*, *M. rotundus* and *M. angulatus*. The analysis confirms the necessity of abandoning *Saracrinus* A. H. Clark (type-species *M. nobilis*), proposed by Gislén (1927). According to Clark (1923), *M. wyvillei* and *M. rotundus* belong to *Metacrinus* sensu stricto (*M. wyvillei* being the type-species) while *M. nobilis* and *M.*

Table 2 Taxonomic significance of symplexial characteristics.

Taxa	Areola:			Crenularium		Interpetaloid zone	
	Mesh shape	Overall shape		Outer edge of petaloid zone	Crenulae of one petaloid zone	Axis	Inner part
	Predominating stereom	On facet	Transverse section				
Metacrinus nobilis	polygonal or round	lanceolate	lanceolate	closed	more than 10	axial groove	differentiated
Metacrinus rotundus				slightly open	less than 10		
Metacrinus wyvillei				closed	more than 10		
Metacrinus angulatus				slightly open	less than 10	closed axial groove	
Cenocrinus asterius		pear-shaped		closed	more than 10	axial groove	undifferentiated
Endoxocrinus parrae				open	less than 8	without axial groove	
Teliocrinus springeri		lanceolate					
Diplocrinus alternicirrus							
Annacrinus wyvillethomsoni							
Neocrinus blakei	diamond-shaped	pear-shaped	pear-shaped	slightly open	8–11	axial groove	
Neocrinus decorus				closed			
Hypalocrinus naresianus		triangular	triangular		more than 11		

Table 3 Taxonomic significance of synostosial characteristics.

Taxa	For one petaloid crenula		Occluded axial canal		Main stereom on interpetaloid zone and crenularium
	Number of culmina	Number of large meshes	Nature of in-filling	Secondary lumen	
Metacrinus nobilis	less than 10	more than 10	meshwork	small	synostosial stereom
Metacrinus rotundus					
Metacrinus wyvillei		less than 30			
Metacrinus angulatus					
Cenocrinus asterius	10–15	irregular width	spicules	large	
Endoxocrinus parrae		25–30	meshwork	small	
Teliocrinus springeri	less than 10	6–10 irregular width			
Diplocrinus alternicirrus			spicules	often fill in	syzygial stereom
Annacrinus wyvillethomsoni			meshwork		
Neocrinus blakei	variable or wanting	10–15	spicules	very large	
Neocrinus decorus	10–15			large	
Hypalocrinus naresianus				small	

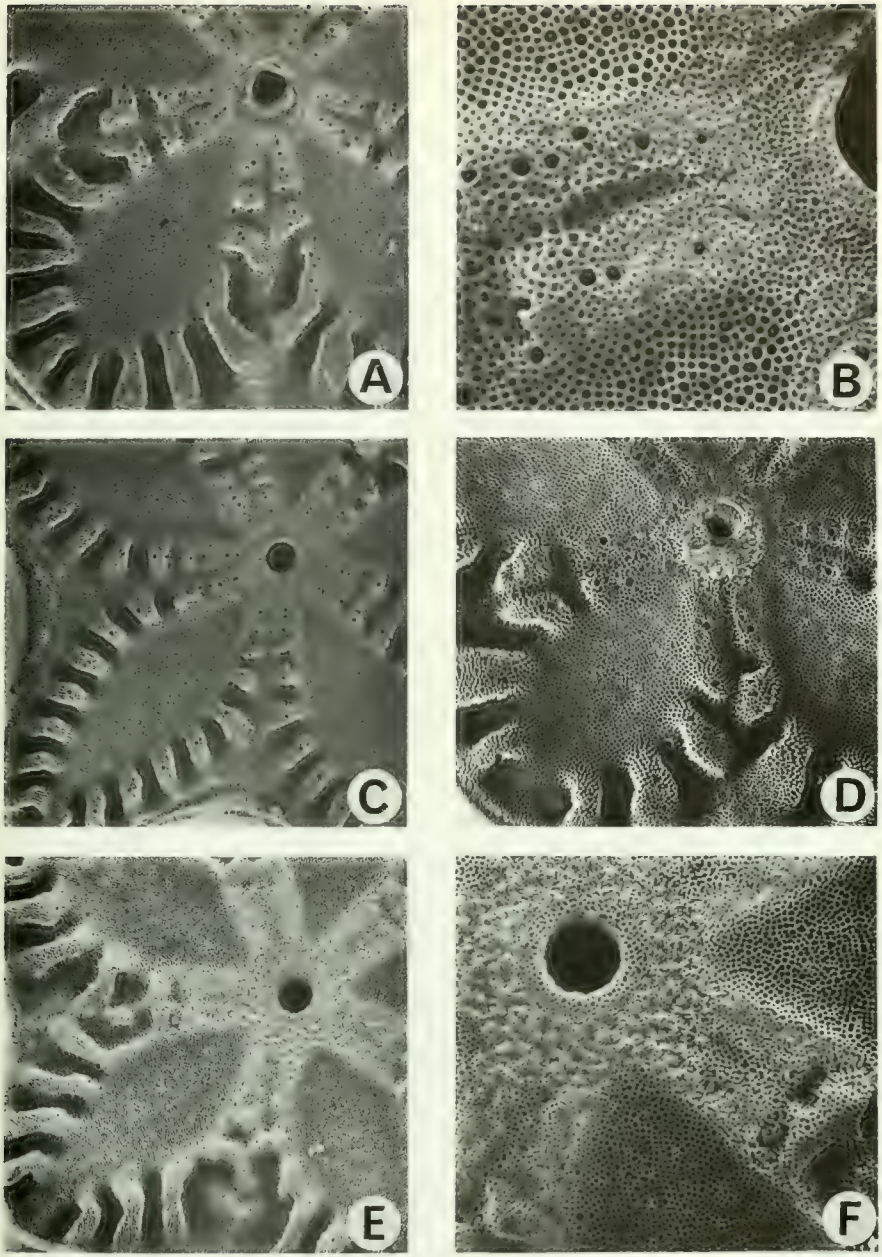

Fig. 3 Stereom of stem joints. (A) *Neocrinus decorus*, α-stereom of the crenularium in growth, showing the spiculata origin of the meshwork, × 750; (B) *Metacrinus nobilis*, synostosial stereom, × 800; (C) *Isselicrinus subbasaltiformis* from the Eocene London Clay, the α-stereom of symplexial areola with numerous large meshes, × 200; (D) *Hypalocrinus naresianus*, α-stereom of symplexial areola with diamond-shaped meshes, × 800; (E) *Metacrinus wyvillei*, α-stereom of symplexial areola with polygonal meshes, × 800; (F) *Endoxocrinus parrae*, α-stereom of symplexial areola with round meshes, × 800.

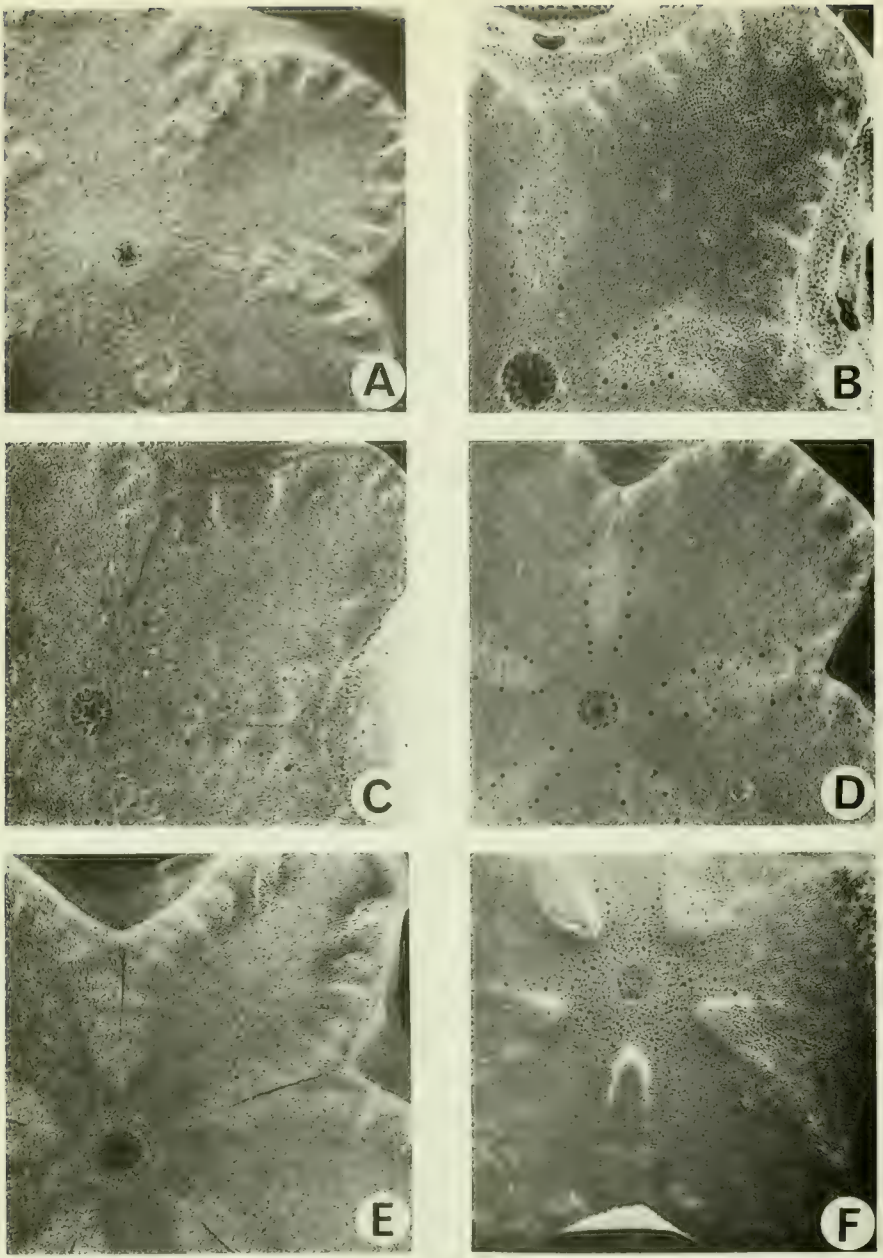

Fig. 4 Symplexial stem joints. (A) *Metacrinus rotundus*, × 18; (B) *Metacrinus rotundus*, inner crenularium with axial groove, × 125; (C) *Metacrinus angulatus*, × 18; (D) *Metacrinus wyvillei*, × 35; (E) *Cenocrinus asterius*, × 18; (F) *Cenocrinus asterius*, inner crenularium with closed axial groove and granulose perilumen, × 45.

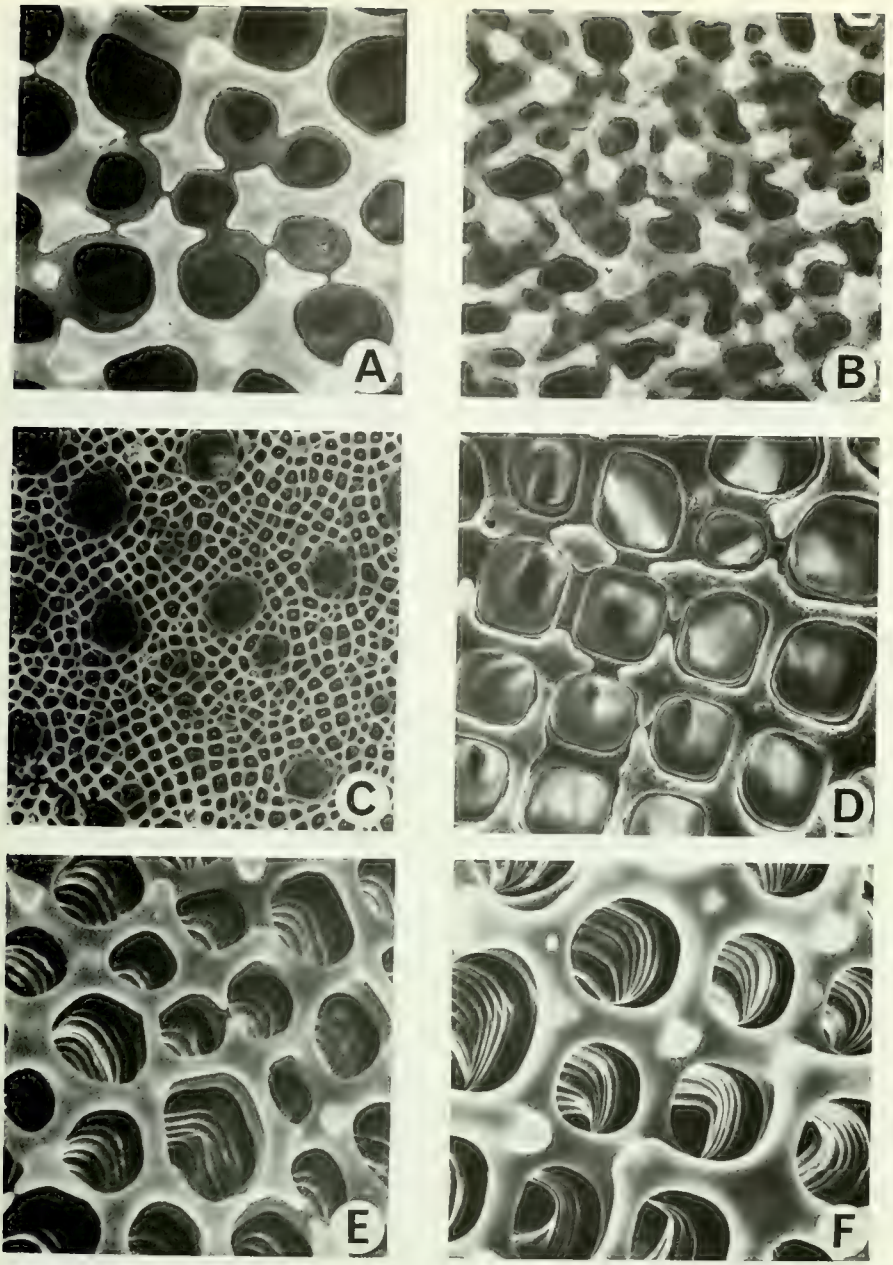

Fig. 5 Symplexial stem joints. (A) *Endoxocrinus parrae*, note the large axial groove of the interpetaloid zone, × 50; (B) *Neocrinus blakei*, × 40; (C) *Neocrinus decorus*, × 30; (D) *Hypalocrinus naresianus*, × 25; (E) *Teliocrinus springeri*, × 45; (F) *Diplocrinus alternicirrus*, × 15.

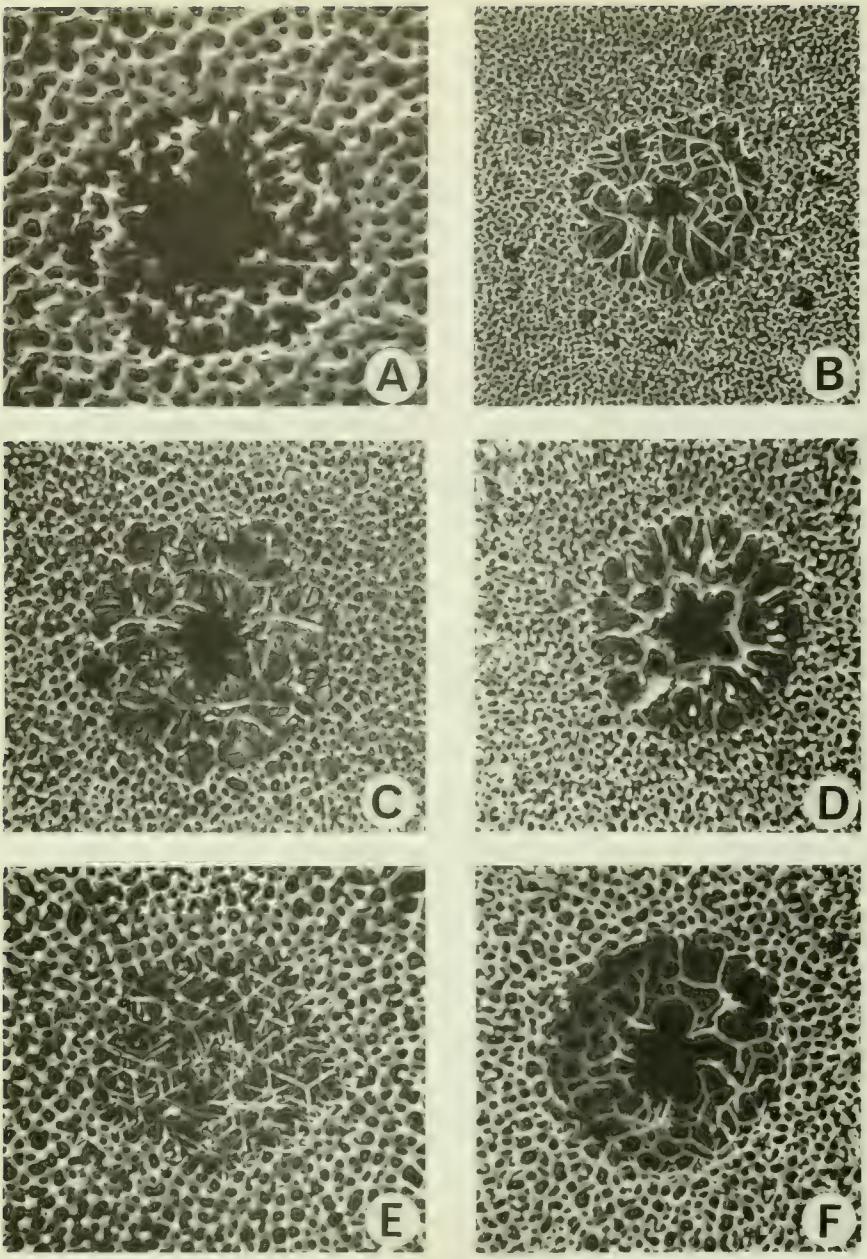

Fig. 6 Synostoses, general view. (A) *Cenocrinus asterius*, ×18; (B) *Neocrinus decorus*, ×35; (C) *Metacrinus wyvillei*, ×30; (D) *Hypalocrinus naresianus*, ×25; (E) *Teliocrinus springeri*, ×30; (F) *Diplocrinus alternicirrus*, radial symmorphy of interpetaloid zones, ×20.

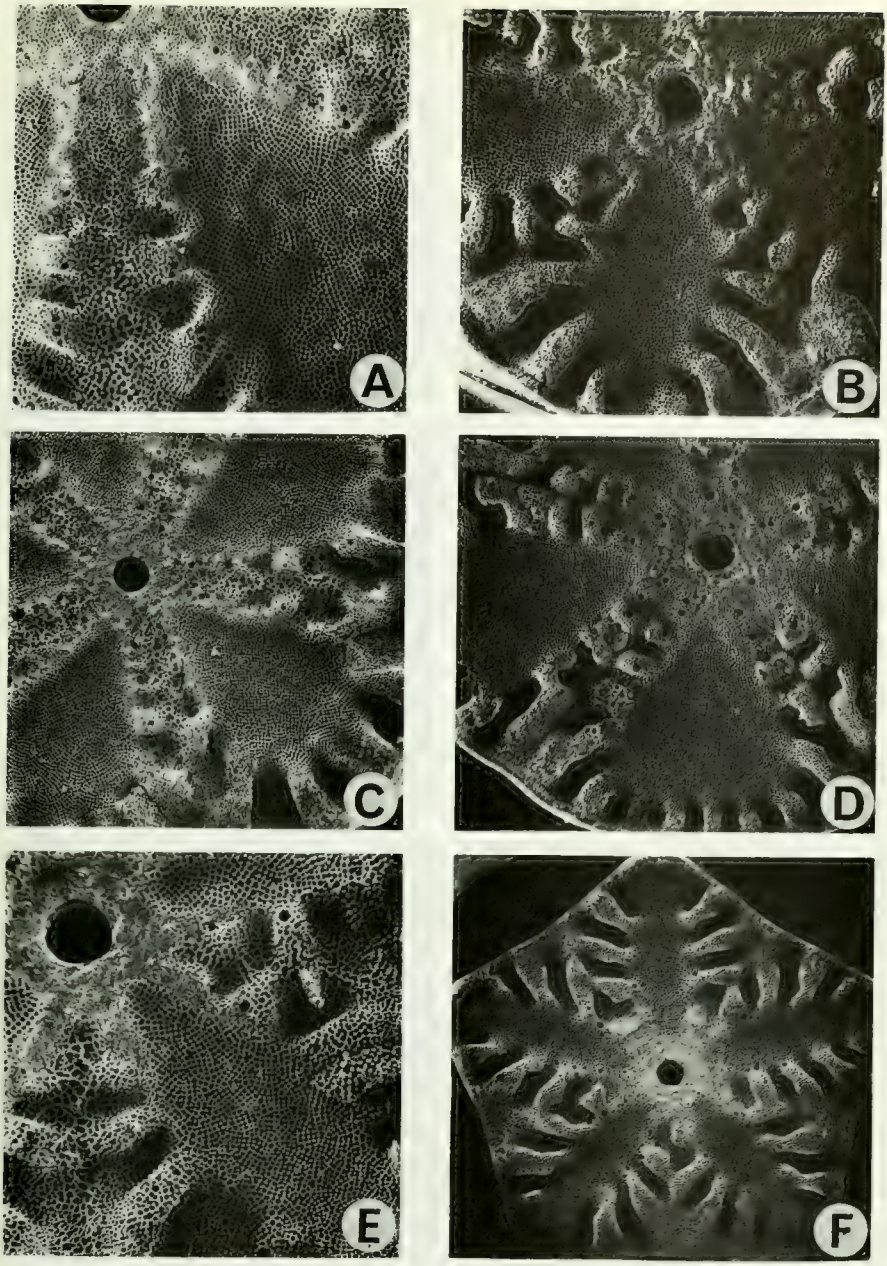

Fig. 7 Synostoses, crenularia and interpetaloid zones. (A) *Teliocrinus springeri*, crenularium with predominating synostosial stereom, × 80; (B) *Hypalocrinus naresianus*, crenularium with predominating syzygial stereom, × 80; (C) *Neocrinus blakei*, interpetaloid zone with predominating syzygial stereom, × 150; (D) *Metacrinus nobilis*, interpetaloid zone with an axial groove, × 150; (E) *Metacrinus angulatus*, interpetaloid zone, × 100; (F) *Diplocrinus alternicirrus*, symmorphial interpetaloid zones, × 50.

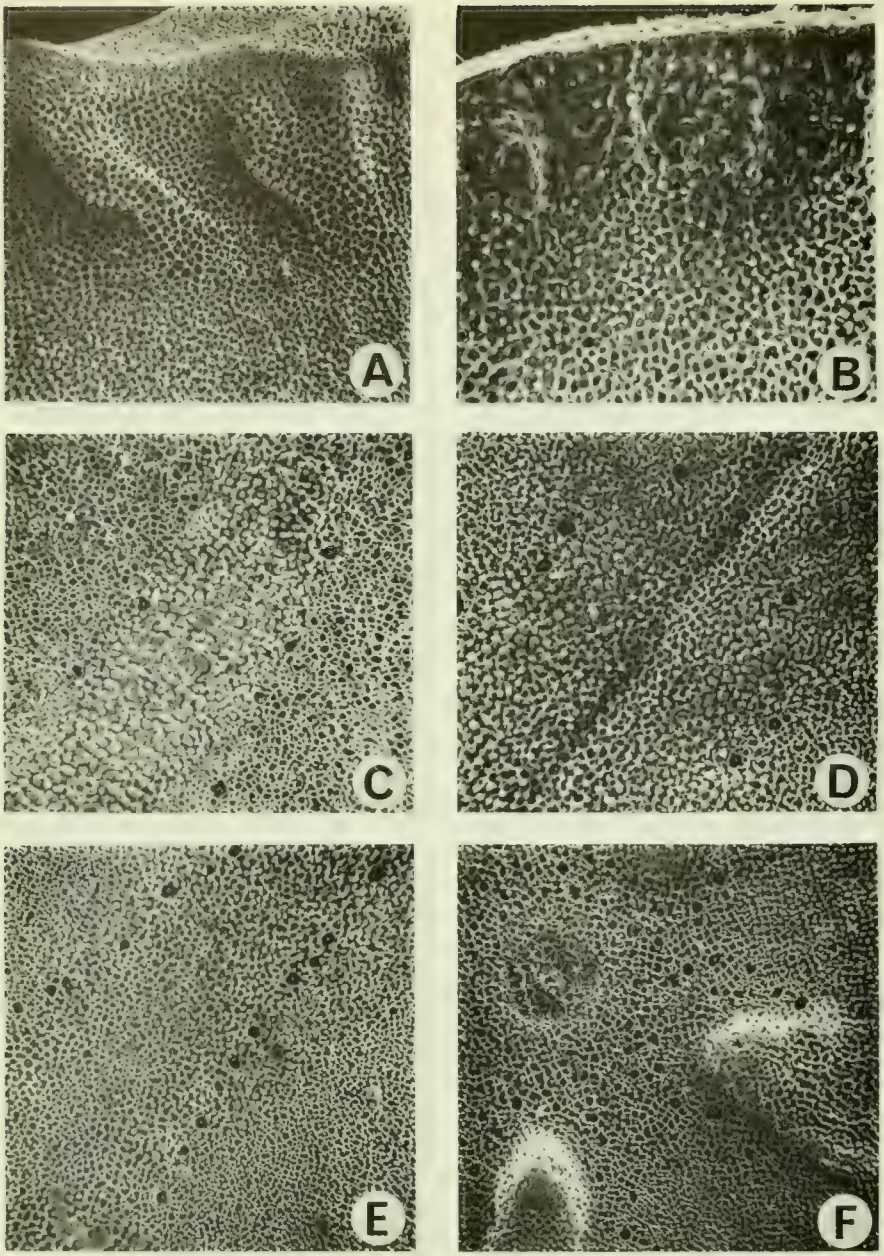

Fig. 8 Synostoses, axial canals. (A) *Cenocrinus asterius*, ×180; (B) *Metacrinus nobilis*, ×100; (C) *Hypalocrinus naresianus*, ×160; (D) *Metacrinus wyvillei*, ×150; (E) *Diplocrinus alternicirrus*, ×160; (F) *Teliocrinus springeri*, ×160.

Table 4 Characteristics common to different genera of Isocrinidae.

	H. n.	*N. d.*	*N. b.*	*A. w.*	*D. a.*	*T. s.*	*E. p.*	*C. a.*	*M. a.*	*M. w.*	*M. r.*	*M. n.*	
	0	0	0	1	1	1	1	2	3	3	3		
M. n.	1 **4**	0 **2**	0 **1**	2 **6**	1 **5**	3 **9**	3 **9**	1 **7**	3 **13**	4 **12**	5 **15**		*M. nobilis*
	3	2	1	3	3	5	5	4	7	5	7		
	0	0	0	1	1	1	1	2	3	3			
M. r.	1 **4**	0 **2**	0 **0**	2 **5**	1 **4**	3 **8**	3 **9**	1 **7**	3 **13**	4 **11**			*M. rotundus*
	3	2	0	2	2	4	5	4	7	4			
	0	0	0	1	1	1	1	2	3				
M. w.	1 **2**	0 **1**	0 **1**	1 **4**	0 **3**	3 **7**	4 **8**	1 **9**	4 **12**				*M. wyvillei*
	1	1	1	2	2	3	3	6	5				
	0	0	0	1	1	1	1	2					
M. a.	1 **2**	0 **1**	0 **0**	1 **4**	0 **3**	3 **7**	4 **8**	1 **7**					*M. angulatus*
	1	1	0	2	2	3	3	4					
	1	1	1	2	2	2	2						
C. a.	0 **3**	0 **4**	1 **4**	1 **5**	2 **6**	1 **5**	1 **5**						*C. asterius*
	2	3	2	2	2	2	2						
	1	1	1	2	2	2							
E. p.	2 **4**	1 **4**	0 **2**	1 **6**	0 **5**	2 **7**							*E. parrae*
	1	2	1	3	3	3							
	1	1	1	2	2								
T. s.	1 **3**	0 **2**	0 **2**	1 **7**	0 **6**								*T. springeri*
	1	1	1	4	4								
	1	1	1	3									
D. a.	2 **4**	2 **4**	2 **5**	4 **13**									*D. alternicirrus*
	1	1	2	6									
	1	1	1										
A. w.	1 **3**	1 **3**	1 **4**										*A. wyvillethomsoni*
	1	1	2										
	2	3											
N. b.	3 **7**	3 **10**											*N. blakei*
	2	4											
	2												
N. d.	4 **8**												*N. decorus*
	2												
H. n.													*H. naresianus*

At the left, detailed numbers of common characteristics, from the top to the bottom for each pair of species: arm, synostosis, symplexy. For synostoses and symplexies characteristics are as in Tables 2 and 3. For arms, they are: IBr 2 ax, division series beyond the first and IBr 2 biconvex shaped (*Neocrinus* and *Hypalocrinus*).

angulatus fall within *Saracrinus*. However, this view is not in accordance with many of the facts, notably the characters provided by the stalk joints.

(4) The main differences between *Metacrinus* and *Cenocrinus* are derived from the synostoses (though these are perhaps not of generic significance) and more importantly the position of the first axillary (at IBr 2 in *Cenocrinus*; beyond IBr 3 in *Metacrinus*). Besides the stalk synostoses, members of the two genera have evident affinities, especially *M. wyvillei* and *C. asterius*, the respective type-species.

(5) *Endoxocrinus* and *Teliocrinus* are clearly distinct genera.

(6) *Diplocrinus* and the monotypic *Annacrinus* possess more common characteristics than do *Metacrinus wyvillei* and the three other species of *Metacrinus* studied. *Annacrinus wyvillethomsoni* can be likened to a *Diplocrinus* adapted for life on mud substrates and is also geographically isolated. Accordingly, it seems best to reduce *Annacrinus* to the rank of a subgenus of *Diplocrinus*.

Key to the recent genera of Isocrinidae based on the morphology of the symplexial stalk joints

1 α-Stereom of areolae predominantly with polygonal or round meshes; transverse section of columnal with lanceolate areas of α-stereom 2
– α-Stereom of areolae predominantly with diamond-shaped meshes; transverse section of columnal with triangular or pear-shaped areas of α-stereom 6
2 Inner part of the crenularium differentiated, outer end closed or slightly open . . . 3
– Inner part of the crenularium undifferentiated 4
3 Axial groove always present on each interpetaloid zone . . . . . ***Metacrinus***
– Closed axial groove on each interpetaloid zone; perilumen granulose . . . ***Cenocrinus***
4 Outer end of the crenularium closed; areolae slightly pear-shaped; 12–14 crenulae to each petaloid zone; interpetaloid axial grooves present . . . . . ***Endoxocrinus***
– Outer end of the crenularium open; areolae always lanceolate 5
5 10 or more crenulae in each petaloid zone; interpetaloid axial grooves present . ***Teliocrinus***
– Less than 8 crenulae in each petaloid zone; no interpetaloid axial grooves ***Diplocrinus*** (including ***Annacrinus***)
6 Less than 11 crenulae in each petaloid zone; areolae lanceolate or pear-shaped . . . 7
– More than 11 crenulae in each petaloid zone; areolae triangular . . . ***Hypalocrinus***
7 Areolae lanceolate; crenularium slightly open; no interpetaloid axial grooves present ***Neocrinus* 1**
– Areolae pear-shaped; crenularium closed; interpetaloid axial grooves present ***Neocrinus* 2**

Synostoses of the material examined

(From the collections of the British Museum (Natural History) unless specified.)

Genus ***METACRINUS*** (including *Saracrinus*)

Metacrinus rotundus Carpenter (Figs 4A, B, 9).
MATERIAL. Japan, B.M. reg. no. 1921.10.4.43–48.
SYNOSTOSES (Fig. 9). More than 40 large meshes in each petaloid zone: outer edge of the facet round: radial symmorphy.

Metacrinus nobilis Carpenter (Figs 3B, 7D, 8B, 10).
MATERIAL. Timor, 1932.12.25.3–5.
SYNOSTOSES (Fig. 10). 30–40 large meshes in each petaloid zone; a few large meshes around the axial canal, loose meshwork extending into the axial canal.

Metacrinus angulatus Carpenter (Figs 4C, 7E, 11).
MATERIAL. Kei Islands, *Challenger* st. 192, 85.3.30.15, para- or syntype.
SYNOSTOSES (Fig. 11). 25–30 large meshes in each petaloid zone; facet stellate, small crenulae at the tip of each petaloid zone, large meshes on a regular line between the petaloid zone and the interpetaloid zone.

Metacrinus wyvillei Carpenter (Figs 3E, 4D, 6C, 8D, 12).
MATERIAL. Kermadec Islands, *Challenger* st. 170A, 85.3.30.16, syntype.
SYNOSTOSES (Fig. 12). Less than 15 large meshes in each interpetaloid zone; secondary lumen stellate with sharp outlines of calcite.

Genus ***CENOCRINUS***

Cenocrinus asterius (Linnaeus) (Figs 4E, F, 6A, 8A, 13).
MATERIAL. Saba Island, West Indies, 84.6.20.1.
SYNOSTOSES (Fig. 13). Large meshes of very irregular width, synostosial areola pear-shaped; thick and irregular spicules extending into the axial canal; secondary lumen large.

Genus ***ENDOXOCRINUS***

Endoxocrinus parrae (Gervais) (Figs 3F, 5A, 14).
MATERIAL. No details, probably West Indies.
SYNOSTOSES (Fig. 14). 25–30 irregular large meshes in each petaloid zone; dense meshwork extending into the axial canal.

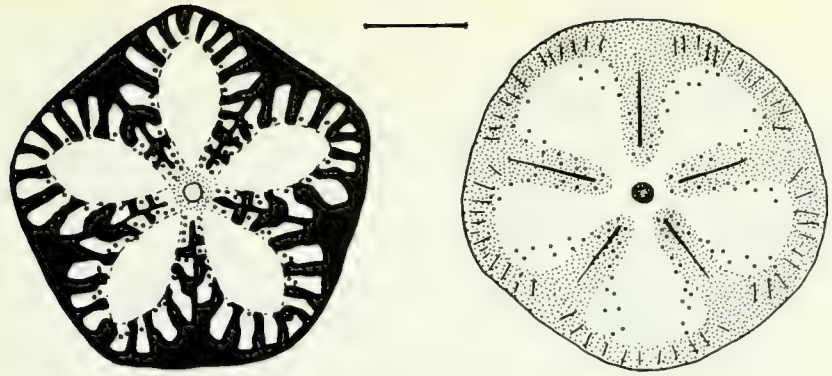

Fig. 9 Stem joints of *Metacrinus rotundus*. (Scale: 2 mm)

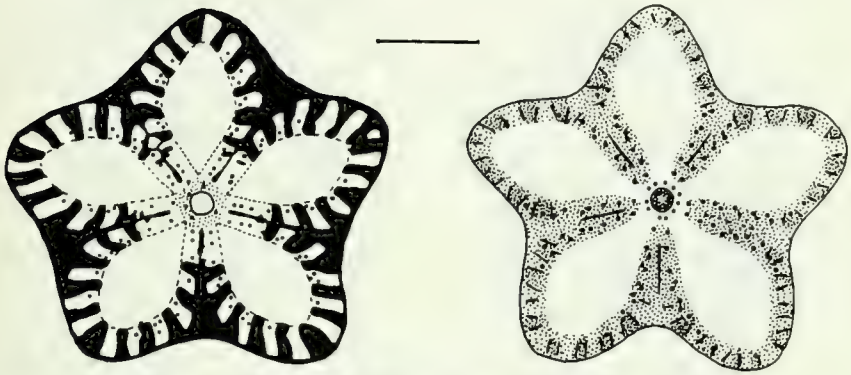

Fig. 10 Stem joints of *Metacrinus nobilis*. (Scale: 2 mm)

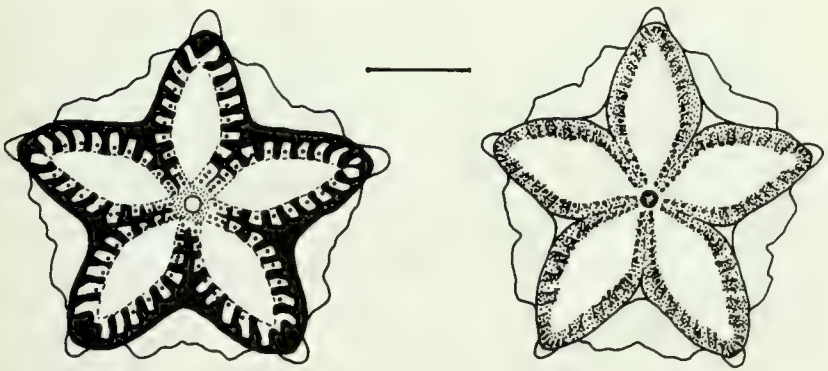

Fig. 11 Stem joints of *Metacrinus angulatus*. (Scale: 2 mm)

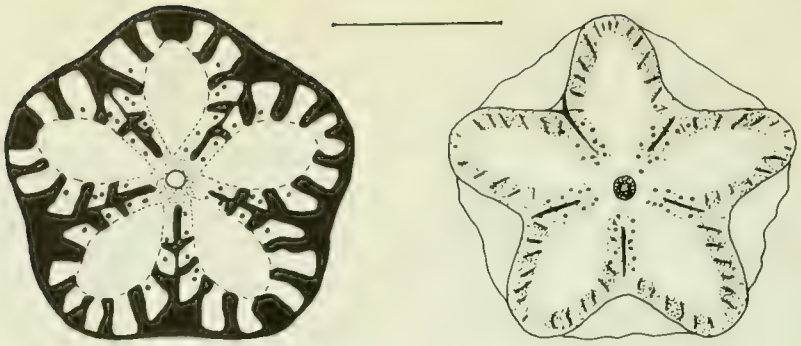

Fig. 12 Stem joints of *Metacrinus wyvillei*. (Scale: 2 mm)

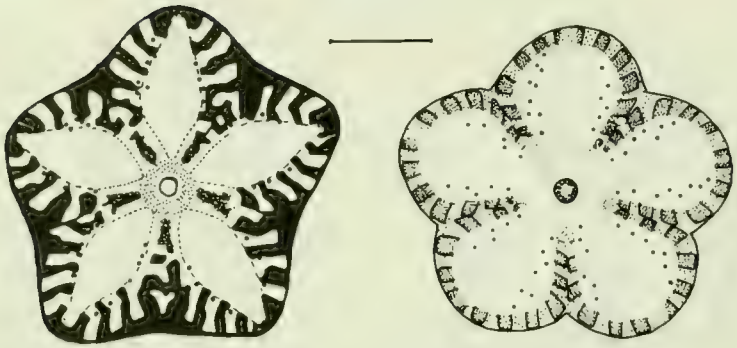

Fig. 13 Stem joints of *Cenocrinus asterius*. (Scale: 2 mm)

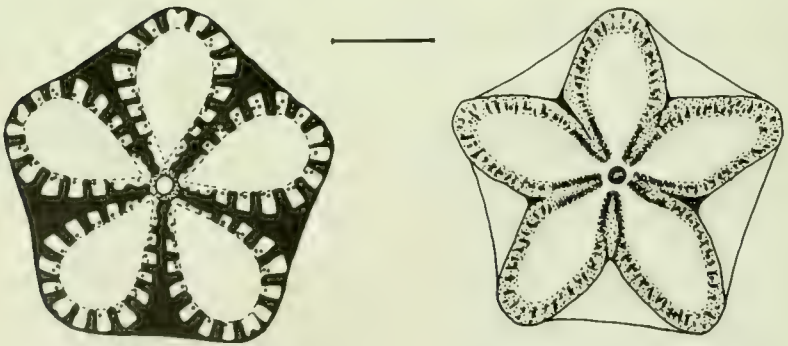

Fig. 14 Stem joints of *Endoxocrinus parrae*. (Scale: 2 mm)

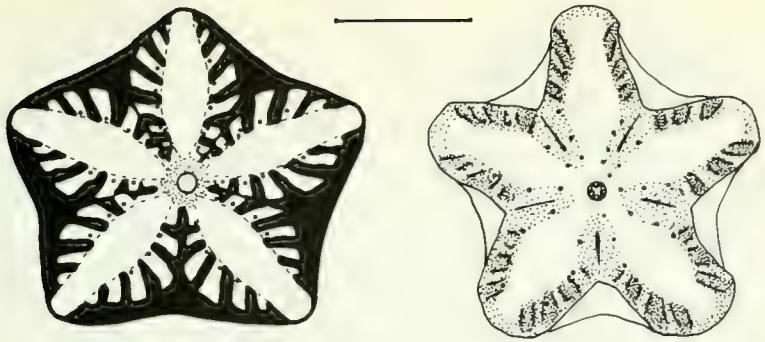

Fig. 15 Stem joints of *Teliocrinus springeri*. (Scale: 2 mm)

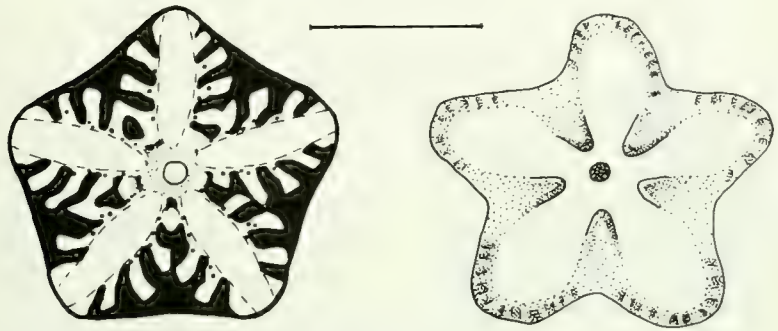

Fig. 16 Stem joints of *Diplocrinus alternicirrus*. (Scale: 2 mm)

Genus ***TELIOCRINUS***

Teliocrinus springeri (Clark) (Figs 5E, 6E, 7A, 8F, 15).
MATERIAL. Madras, 1932.12.25.2.
SYNOSTOSES (Fig. 15). 10 or less large meshes in each petaloid zone: general symmorphy well developed.

Genus ***DIPLOCRINUS*** (including *Annacrinus*)

Diplocrinus alternicirrus (Carpenter) (Figs 5F, 6F, 7F, 8E, 16).
MATERIAL. Meangis Islands (N. Moluccas), *Challenger* st. 214, 85.3.30.22, syntype.
SYNOSTOSES (Fig. 16). Radial symmorphy of interpetaloid zones well developed; axial canal completely filled by thin spicules; small crenulae consisting of thick syzygial β-stereom.

Diplocrinus (Annacrinus) wyvillethomsoni (Jeffreys *in* Wyville Thomson) (Fig. 17; see also Roux, 1971 and 1974).
MATERIAL. Bay of Biscay, *Thalassa* st. Z452, Muséum National d'Histoire Naturelle, Paris.
SYNOSTOSES (Fig. 17). Radial symmorphy poorly developed; axial canal completely filled with relatively dense meshwork, a few outer crenulae rectangular with a thick syzygial stereom.

Genus ***NEOCRINUS***

Crenularium and interpetaloid zones with syzygial β-stereom, 10–15 large meshes in each petaloid zone of synostoses.

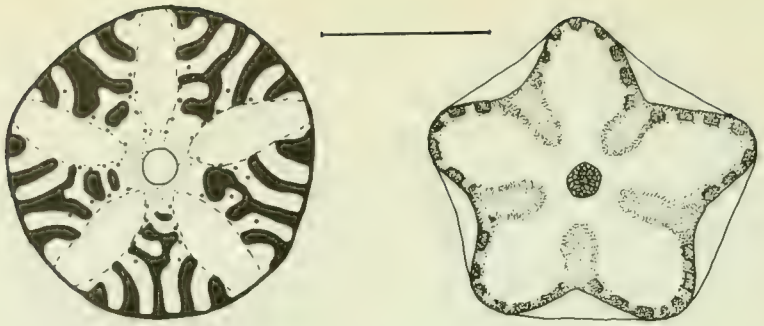

Fig. 17 Stem joints of *Diplocrinus* (*Annacrinus*) *wyvillethomsoni*. (Scale: 2 mm)

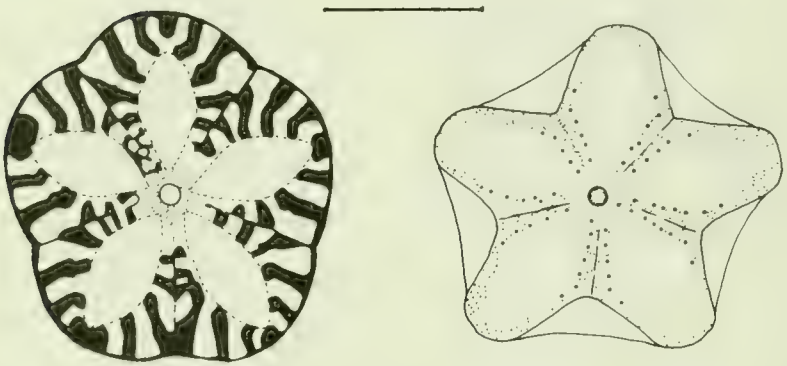

Fig. 18 Stem joints of *Neocrinus blakei*. (Scale: 1 mm)

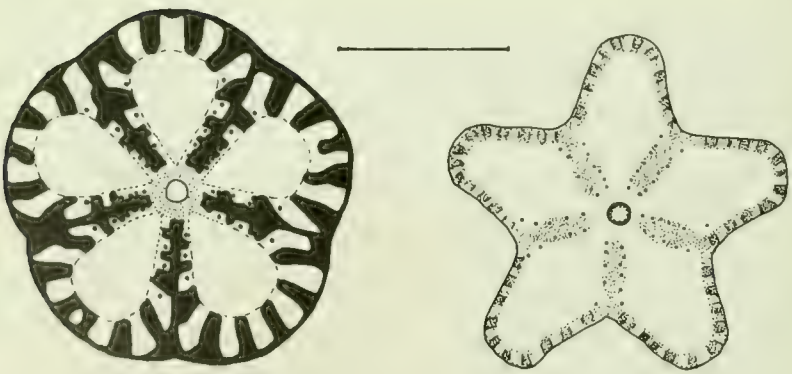

Fig. 19 Stem joints of *Neocrinus decorus*. (Scale: 2 mm)

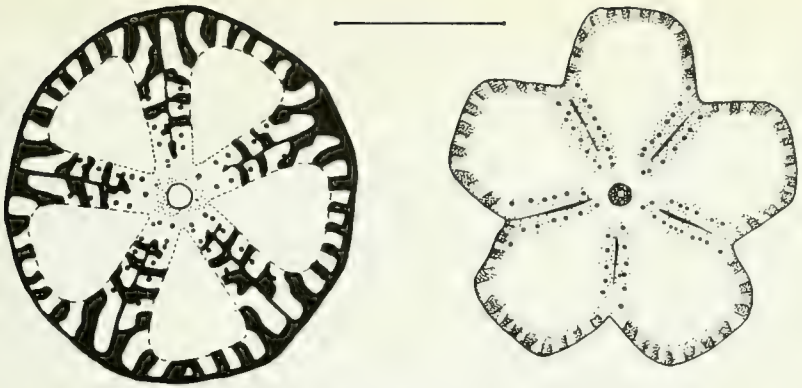

Fig. 20 Stem joints of *Hypalocrinus naresianus*. (Scale: 2 mm)

Neocrinus blakei (Carpenter) (*Neocrinus* 1) (Figs 5B, 7C, 18).
MATERIAL. Cuba, West Indies, 1939.6.15.1.
SYNOSTOSES (Fig. 18). Crenularium reduced or wanting; axial canal largely open with a few secondary spicules.

Neocrinus decorus (Wyville Thomson) (*Neocrinus* 2) (Figs 3A, 5C, 6B, 19).
MATERIAL. Saba Island, West Indies, 84.6.20.5.
SYNOSTOSES (Fig. 19). Crenularium well developed; axial canal filled in with irregular spicules; secondary lumen large.

Genus ***HYPALOCRINUS***
(Main characters like *Neocrinus*)

Hypalocrinus naresianus (Carpenter) (Figs 3D, 5D, 6D, 7B, 8C, 20).
MATERIAL. Timor, 1916.6.20.6.
SYNOSTOSES (Fig. 20). Crenularium well developed; axial canal filled in with dense spicules; secondary lumen small.

Conclusions

The characters of the stalk joints of the Isocrinidae are of taxonomic significance. The symplexial articulations indicate relationships between species belonging to the same genus, or affinities between different genera, independent of variations in external morphology. This conclusion is very useful for the study of comparative morphology of both recent and fossil genera. According to the characteristics shown by the stalk, it is likely that *Hypalocrinus naresianus* could be regarded as a recent representative of the mesozoic genus *Balanocrinus*, the crown of which is so far unknown. However, the converse presence of the fossil genus *Isocrinus* in the recent fauna is not supported by the present evidence. This problem will be reviewed later. More detailed studies are necessary to confirm differences or affinities between the various taxa of the Isocrinidae. I plan next to observe the facet ontogeny from proximal to distal in the stalk and from young to senile specimens and to relate the results to similar studies on the joints of division series and arms.

Finally a new classification suggested by the stalk joint characteristics is given below.

Family **ISOCRINIDAE**
Subfamily I
genus ***Metacrinus*** (*sensu* Carpenter)
type-species: *M. wyvillei*

genus ***Cenocrinus***
type-species: *C. asterius*
genus ***Teliocrinus***
type-species: *T. springeri*
genus ***Endoxocrinus***
type-species: *E. parrae*
genus ***Diplocrinus***
subgenus ***Diplocrinus*** (*Diplocrinus*)
type-species: *D.* (*Diplocrinus*) *maclearanus*
subgenus ***Diplocrinus*** (*Annacrinus*)
type-species: *D.* (*Annacrinus*) *wyvillethomsoni*

Subfamily II
genus ***Hypalocrinus***
type-species: *H. naresianus*
genus ***Neocrinus* 1** (not synonym of fossil *Isocrinus*)
type-species: *N. blakei*
genus ***Neocrinus* 2** (*Neocrinus sensu* Rasmussen)
type-species: *N. decorus*

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7 OCT 1977

New names are not given for subfamilies I and II or for *Neocrinus* 1 and 2 because the diagnoses should include detailed studies of arm joints.

Acknowledgements

I am indebted to Miss A. M. Clark, who provided most of the material used in this study, and to the Trustees of the British Museum (Natural History) for the opportunity to publish this paper.

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—— 1974. Observations au microscope électronique à balayage de quelques articulations entre les ossicules du squelette des crinoides pédonculés actuels (Bathycrinidae et Isocrinina). *Trav. Lab. Paléont. Orsay*, Nov. **1974** : 1–10, 4 pls, 3 figs.

—— 1975. Microstructural analysis of the crinoid stem. *Paleont. contr. Univ. Kans.* **75** : 1–7, 2 pls, 5 figs.

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Notes on the anatomy and classification of elopomorph fishes

P. H. Greenwood

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London 1977

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Notes on the anatomy and classification of elopomorph fishes

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Introduction

Little detailed information is available on the cranial musculature of elopomorph fishes, a gap in our knowledge which was brought home when recently I was asked to comment on the possible significance of a bony bridge on the angulo-retroarticular of *Albula vulpes* (Nybelin, 1976).

From this initial involvement with *Albula* my interest turned to its supposed near relative, *Pterothrissus*. The nature of the similarities and differences I found in the musculature of these genera led me to consider the possible use of jaw muscles in testing some of the views expressed on the phylogeny and classification of the Elopomorpha (see Forey, 1973a & b; Nelson, 1973; McDowell, 1973; Gosline, 1971). This objective necessitated the investigation of jaw muscles in other elomorphs, especially the Notacanthiformes and Anguilliformes (both taxa *sensu* Greenwood, Rosen, Weitzman & Myers, 1966). McDowell's (1973) magnificent review of the Heteromi (=Notacanthiformes) includes some brief descriptions and comments on notacanth and halosaur jaw muscles. These I sometimes found in conflict with my own observations (and interpretations), thus highlighting the need for further detailed and illustrated descriptions of the musculature and

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associated osteological features in these fishes as well as in the more basal members of the superorder. Amongst the osteological features may be mentioned the peculiarities of the palatopterygoid arch in notacanthiforms, in particular the specialization of the autopalatine suggested by McDowell (another area where an alternative explanation seems more probable).

The results of these comparative anatomical studies have provided new information which I believe can be used to throw light on the phyletic relationships and hence classification of the Elopomorpha.

Disappointing in this respect was the information obtained from the jaw musculature of the Anguilliformes. My preliminary investigations show that, although highly specialized in some details, the anguilliform 'bauplan' is essentially that of a basic elopomorph such as *Elops*.

Material examined

D = dissected; E = examined; SL = standard length; TL = total length.
BMNH (British Museum (Natural History)); JLBS (J. L. B. Smith Institute of Ichthyology); MCZ (Museum of Comparative Zoology, Harvard); VMS (Virginia Institute of Marine Science).

Albula vulpes (D), BMNH 1923.7.30 : 47–51. Rio de Janeiro. 188 mm SL.
Albula vulpes (D), BMNH 1932.2.8 : 5. Trinidad. 180 mm SL.
Albula vulpes (D), Gothenburg Museum. (Head only.)
Aldrovandia affinis (D), 'Discovery' Stn 7853, 25° 51·7′ N, 16° 2·4′ W, 1518–1503 m. 2 specimens, 290 mm SL; 223 mm (tail missing).
Aldrovandia gracilis (D), 'Discovery' Stn 7857, no. 5, 36° 46·6′ N, 14° 31′ W, 1356–1341 m. 1 specimen, 280 mm (tail broken).
Aldrovandia phalacra (D), 'Discovery' Stn 7853 (details above). 2 specimens, 320 mm & 365 mm TL.
Amia calva (D), BMNH unregistered specimen. Illinois, U.S.A. Head only, 50 mm.
Anguilla anguilla (D), BMNH 1962.6.29 : 11–42. Isle of Man. 210 & 276 mm TL.
Conger conger (D), BMNH 1962.6.29 : 45. Isle of Man. 425 mm TL.
Elops saurus (D), BMNH 1932.11.10 : 3–4. Berbice, Guyana. 180 mm SL.
Elops senegalensis (D), Gothenburg Museum. Bathurst, Gambia. Head only, 74 mm from a specimen 325 mm SL.
Halosaurus guentheri (D), BMNH 1966.10.14 : 1–2. 'Oregon' Stn 4375. 230 mm (tail missing) & 360 mm TL.
Halosauropsis macrochir (D), 'Discovery' Stn 8512, no. 4, 2281-2465 m. 1 specimen 556 mm TL.
Lipogenys gilli (D), MCZ 38322. 'Capt. Bill II' Stn 134, 38° 05′ N, 73° 43′ W. 337 mm SL.
Lipogenys gilli (D), MCZ 37612. 'Capt Bill II' Stn 95, 42° 45′ N, 63° 47′ W. 255 mm SL.
Lipogenys gilli (D), VMS 03465. 36°40·9′ 41 6′ N, 74° 38·5′–35·2′ W, 1111 m. 212 mm SL.
Lipogenys gilli (E), VMS 03467. 36°42·5′–44·0′ N, 74°32′–30·9′ W, 1190 m. 227 mm SL.
Lipogenys gilli (E), VMS 03466. 37° 00·0′–00·2′ N, 74° 19·0′–17·6′ W, 1698 m. 230 mm SL.
Notacanthus sexspinis (E), BMNH 1873.12.13 : 27. Wellington. Skeleton in alcohol.
Notacanthus sexspinis (E), BMNH 1872.4.26 : 14. Wellington. 375–420 mm SL.
Notacanthus bonapartei (D), BMNH 1972.1.26 : 33–39. Off W. Ireland. 340 & 450 mm SL.
Polyacanthonotus africanus (E), 'Discovery' Stn 7853, 25°51·7′ N, 16°2·4′ W, 1518–1503 m. 123 mm TL.
Polyacanthonotus africanus (D), 'Discovery' Stn 8519, no. 7, 24°2·2′ N, 16°59·2′ W, 1037–997 m. 186 mm TL.
Polyacanthonotus rissoanus (D), 'Discovery' Stn 8512, no. 4. 2281–2465 m. 293 mm TL.
Polyacanthonotus rissoanus (E), BMNH 1904.3.4 : 3. Off Cape Point. 297 mm TL.
Pterothrissus belloci (D), JLBS 3677. No locality stated. 132 mm SL.
Pterothrissus gissu (E), BMNH 1879.5.14 : 532 Mosina. (Holotype of *Bathythrissa dorsalis*.) 380 mm SL.
Pterothrissus gissu (E), BMNH 1903.5.14 : 142. Japan. Skeleton
Pterothrissus gissu (D), BMNH 1977.1.22 : 3. Japan. 315 mm SL.

In addition to all the above the following specimens were radiographed:

Aldrovandia gracilis, BMNH 1966.10.4 :3.
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Aldrovandia phalacra, BMNH 1960.1.15 :2
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Halosaurus parvipinnis, BMNH 1939.5.24 : 660–661.
Halosaurus oweni, BMNH 1890.6.16 : 55.

Abbreviations used in the figures

A1α:	A1α division of the adductor mandibulae muscle
A1α¹ ⎫ A1α² ⎭	Superficial and deep subdivisions, respectively, of adductor mandibulae division A1α
A1β:	Maxillary division (A1β) of the adductor mandibulae muscle
A2:	A2 division (mandibular) of the adductor mandibulae muscle
A2¹:	Muscle slip from A2
A2α ⎫ A2β ⎭	Deep and superficial subdivisions, respectively, of adductor mandibulae A2 division
A3:	A3 division of the adductor mandibulae muscle
AbdM:	Abductor muscles of the pectoral fin
AdHy:	Adductor hyomandibulae muscle
Ad Mand:	Adductor mandibulae (undivided muscle mass)
Ad Op:	Adductor operculi muscle
Ant hyl:	Anterohyal (Anterior ceratohyal)
Ap Pmx:	Ascending process of premaxilla
Aω:	Intramandibular (Aω) division of the adductor mandibulae muscle
? Aω:	Tendon thought to be remnant of Aω muscle
BBr:	Bony bridge of the angulo-retroarticular
C Emax-Pmx:	Combined ethmomaxillary and ethmopremaxillary ligaments
Ct:	Connective tissue
Ct nod:	Connective tissue nodule
D Ct nod:	Drogue-shaped connective tissue nodule
D Emax:	Deep ethmomaxillary ligament
D Op:	Dilatator operculi muscle
D pal:	Dermopalatine
Ectp:	Ectopterygoid
E Max:	Ethmomaxillary ligament
End Pg:	Endochondral pectoral girdle
Entp:	Entopterygoid
Epal:	Ethmopalatine ligament
E Pmx:	Ethmopremaxillary ligament
Epx:	Epaxial body musculature
Fac:	Facet for articulation with the parasphenoid
Hyh:	Hyohyoideus muscle
Hyom:	Hyomandibula
Hypx:	Hypaxial body musculature
Ihy:	Interhyal
Lap:	Levator arcus palatini muscle
Lap D ⎫ Lap S ⎭	Deep and superficial parts, respectively, of the levator arcus palatini muscle
LE Pmx:	Lateral ethmopremaxillary ligament
Lig Pri:	Ligamentum primordium
L Op:	Levator operculi muscle
Max:	Maxilla
Max-Pmx:	Maxillo-premaxillary ligament
Metp:	Metapterygoid
Nub:	Nubbin of cartilage
Op:	Operculum
Op ara:	Opercular-angulo-retroarticular ligament
Op met:	Opercular-metapterygoid ligament
P:	Autopalatine
? P:	Presumed autopalatine
PecF:	Pectoral fin
Phy:	Protractor hyoideus muscle
Phyc:	Pharyngoclavicularis muscle
P lig:	Posterior maxillo-mandibular ligament
P Max 1:	Palatomaxillary ligament
Pmx:	Premaxilla

PPmx 1:	Palato-premaxillary ligament
Pthyl:	Posterohyal (Posterior ceratohyal)
Q:	Quadrate
SE Max 1:	Superior ethmomaxillary ligament
So Lig P:	Suborbital branch of ligamentum primordium
Sthy M:	Sternohyoideus muscle
Symp:	Symplectic
T:	Tendon
TA1α^2:	Tendon from adductor A1α^2 muscle
TA1β:	Tendon from adductor A1β muscle
TAβ+2:	Shared tendon of adductor A1β and A2 muscles
TA1β+A2β:	Shared tendon of adductor A1β and A2β muscles
TA2β:	Tendon from adductor A2β muscle
TD:	Ligament from dentary joining tendon from adductor A1β muscle
Tp:	Tooth plate on ectopterygoid
T Sthy:	Tendon from sternohyoid muscle to hyoid arch
UE Pmx:	Upper ethmopremaxillary ligament
Vhyl:	Ventrohyal

Jaw and associated muscles and ligaments

I. ALBULIDAE, PTEROTHRISSIDAE and HALOSAURIDAE

PTEROTHRISSIDAE

Pterothrissus belloci Cadenat

Since the specimens available for dissection had suffered some damage to the snout region, only the jaw muscles will be described. The jaw ligaments are described from a specimen of *P. gissu* (p. 69).

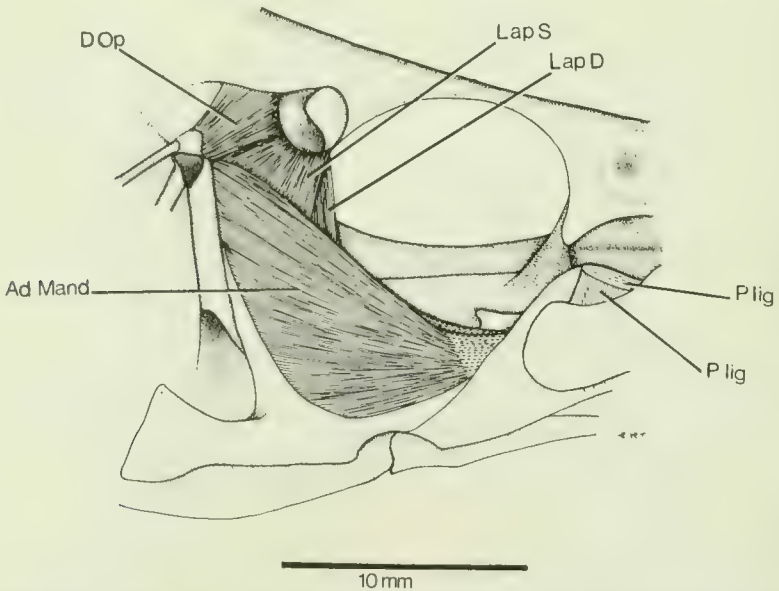

Fig. 1 *Pterothrissus belloci*. Jaw musculature in right lateral view. The supramaxilla has been removed to show the maxillo-mandibular ligaments. Drawn by Miss E. Tarr from specimen RUSI 3674, 13·8 cm standard length.

ADDUCTOR MANDIBULAE MUSCLES (Fig. 1). The adductor is a single muscle mass originating on the preoperculum and metapterygoid. Anteriorly it inserts through a fairly well-developed and deep tendon onto the posterior margin of the compound angulo-retroarticular bone at about its mid-point. Ventral to this point of insertion there appears to be another, effected through an area of much looser connective tissue.

On the medial face of the main adductor muscle mass the Aω portion arises from an extensive tendinous aponeurosis (Fig. 2). Muscle Aω deepens as it runs forward so that it comes to occupy almost the entire Meckelian fossa, in which it has its insertion.

Apart from the fact that no fibres of the adductor mandibulae are inserted onto the maxilla, this muscle in *Pterothrissus* closely resembles that of *Elops saurus* (see Vrba, 1968). The maxillo-mandibular ligaments of *Pterothrissus*, however, are quite different since there is no typical ligamentum primordium in this genus. In *Elops* there is what can be considered a typical lower teleostean ligamentum primordium (see Winterbottom, 1974 : 232), as well as a posterior ligamentous connection between the maxilla and the lower jaw. I would interpret the latter as being homologous with the only ligaments present in *Pterothrissus*, which, therefore, does not have a true ligamentum primordium.

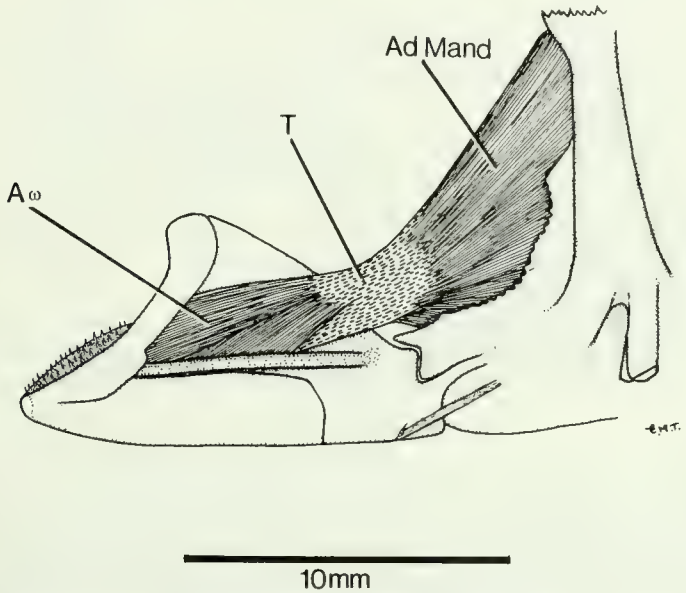

Fig. 2 *Pterothrissus belloci.* Medial aspect of right lower jaw. Drawn by Miss E. Tarr; same specimen as in Fig. 1.

LEVATOR ARCUS PALATINI MUSCLE. This is a moderately large muscle originating from the pterotic and sphenotic regions of the skull (Fig. 1). Its main body is subdivided, one set of fibres running obliquely backwards and downwards to insert medially on the metapterygoid. The other part of the muscle runs almost vertically downwards to insert dorso-anteriorly on the lateral face of the metapterygoid.

ADDUCTOR ARCUS PALATINI MUSCLE. A few fibres representing this muscle are found in the connective tissue linking the pterygoid arch with the parasphenoid.

Pterothrissus gissu Hilgendorf

MAXILLO-MANDIBULAR LIGAMENTS. The *ligamentum primordium* is long and strap-like, and com-

posed of rather loose and thin connective tissue. It extends from a point at about the middle of the angulo-articulo-retroarticular near its ventral margin to the head of the maxilla; it inserts laterally on that bone near the base of the short ascending head. Since the ligament passes laterally over the dorso-posterior angle of the maxilla it binds that bone closely to the lower jaw. The origin of the ligament on the lower jaw is not marked by any noticeable protuberance.

There are two other ligamentous connections between the maxilla and the lower jaw. A broad, sub-triangular ligament runs from just below the coronoid process of the lower jaw to the inner aspect of the maxilla posteriorly. It attaches to that bone immediately below its line of articulation with the supramaxilla. A second, and narrower but denser, ligament extends from the crown of the coronoid process horizontally forward to the upper margin of the maxilla, inserting just anterior to the region of the supramaxillary articulation.

Other jaw ligaments. A long and stout *ethmopremaxillary* ligament runs from the dorso-lateral aspect of the dermethmoid to the premaxilla, attaching dorsally near the base of its ascending process. At its origin on the ethmoid the ligament is confluent with a similar *ethmomaxillary* one which is distinct from but closely applied to the ethmopremaxillary ligament over the posterior two-thirds of its length. The ethmomaxillary ligament attaches to the maxilla at a ventral point immediately below the ascending head of that bone.

A very short and small *maxillopremaxillary* ligament is present, linking the two bones at the point where the premaxilla passes medial to the maxilla.

From the inner aspect of the first infraorbital bone, a long and compact ligament runs down to the maxilla, attaching near the head of that bone and also attaching to the sesamoid cartilage lying between the palatine and the articulating surface of the maxilla.

An extensive sheet of tough connective tissue closely binds the dorsal dome of the sesamoid cartilage to the ascending head of the maxilla; it is probably homologous with the palatomaxillary ligament found in other elopoids (see Forey, 1973a : fig. 3).

According to Forey (1973a : 355) *Pterothrissus* has the same complement of jaw ligaments as do *Elops* and *Tarpon*, a statement with which I would agree, except that in the specimen I dissected no trace of a palatopremaxillary ligament could be found.

Jaw muscles. The arrangement and morphology of the jaw muscles in *P. gissu* are identical with those described above for *P. belloci* (see Fig. 1). However, in the specimen I dissected (315 mm SL) the adductor mass does show the incipient separation of a smaller, dorsomedial section.

ALBULIDAE

Albula vulpes (L).

Maxillo-mandibular ligaments. The *ligamentum primordium* is an inverted Y-shaped ligament (Fig. 3) with its stem attached anteriorly to a dorsally directed process of the maxilla lying above and lateral to the insertion point of a tendon from the adductor mandibulae muscle (see below, p. 71). The lower and broader of the Y's two arms is attached to the supramaxilla; the upper arm continues much further posteriorly, and attaches at the base of the bony bridge on the angulo-retroarticular (Fig. 3). This arm of the ligament also has a small area of attachment on the dorsal margin of the coronoid process.

In the smallest of the three specimens dissected (BMNH 1932.2.8 : 5; 108 mm standard length), the ligamentum primordium is poorly differentiated from the other fibres of the connective tissue through which it runs. In the largest fish (Gothenburg Museum specimen) the ligament is thick, almost fleshy and readily distinguishable. In neither specimen is there any sign of muscle fibres from the adductor mandibulae complex inserting onto the ligamentum primordium.

Other jaw ligaments. A vertical *ethmopremaxillary* ligament runs from the dermal ethmoid to the head of the ascending premaxillary arm, and a broad, rather diffuse and horizontally aligned *ethmomaxillary* ligament connects the dermethmoid with the incurved part of the maxillary head. The maxilla is connected to the premaxilla through a short ligament (the *maxillopremaxillary*) running from the curve of the maxillary head to the premaxilla at a point slightly behind the base

of its ascending process. Another ligament, the *palatomaxillary*, runs from the head of the autopalatine bone to the sesamoid cartilage interposed between the palatine and the maxilla; this ligament apparently continues around the posterior face of the cartilage (to which it is very closely applied) and inserts onto the maxilla itself.

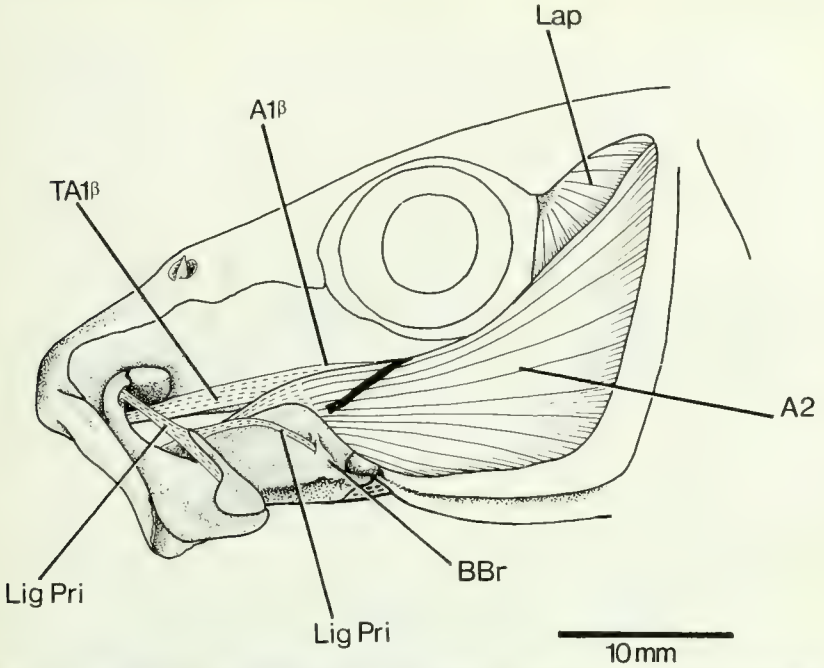

Fig. 3 *Albula vulpes*. Jaw musculature and ligaments in left lateral view. Specimen BMNH 1932.2.8 : 5.

ADDUCTOR MANDIBULAE MUSCLES (Figs 3 & 4). The adductor complex is a rather flat, not noticeably voluminous muscle mass. It shows no clear-cut subdivisions, except for a single tendinous slip which arises dorsomedially near the region of the muscle's insertion onto the dentary. From here it runs forward to insert, tendinously, onto the maxilla a little behind its palatine head (Figs 3 & 4). The few muscle fibres associated with the origin of the tendon are barely separable, as an elongate torpedo-shaped aggregate, from the main body of the muscle.

By definition (see Winterbottom, 1974 : 232) this ill-defined muscle should be identified as section A1 of the adductor complex. However, it must be stressed that the muscle in *Albula* does not appear to have '. . . developed from the dorsal enroachment of the fibres of A2 along the primordial ligament . . .' (Winterbottom, 1974 : 232) because an apparent ligamentum primordium, completely unconnected with any part of the adductores, is also present (see above).

This dorsal segment of the adductor in *Albula* seems to be homologous with the A1β division of that muscle in Halosauridae (and Notacanthidae); see below. Hence, it will be given the same designation in this species, viz. A1β.

The remaining and major part of the adductor mass in *Albula* is identified as an A2 muscle, principally because it has the same relationships with the lower jaw as does the A2 division in other fishes (see Winterbottom, 1974 : 233–234).

Almost at its origin the tendon of A1β bifurcates, the upper portion continuing forward to the maxilla, the lower portion running downwards at a steep angle. This division soon expands into a broad, deltoid sheet (Fig. 4). Some fibres of the main A2 muscle attach to this sheet dorsally,

whilst anteriorly it serves as an aponeurotic origin for a thin, triangular muscle which inserts into the Meckelian fossa. Because of its origin and insertion, this muscle is identified as the Aω division of the adductor complex. The posterior part of the muscle-tendon sheet remains tendinous and inserts, rather narrowly, onto the ventral margin of the dentary, a little before its suture with the angulo-retroarticular bone (Fig. 4).

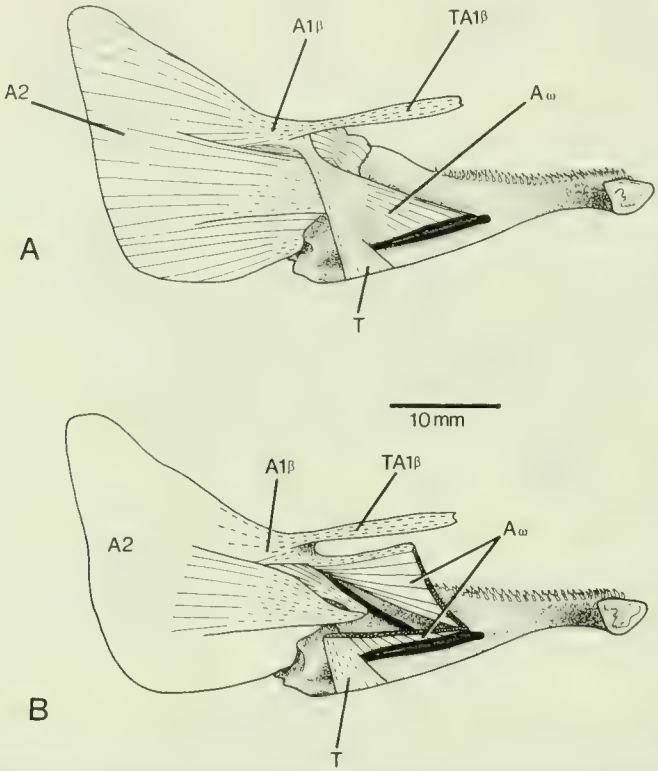

Fig. 4 *Albula vulpes*. Musculature associated with the lower jaw; left side, medial aspect. (A) The muscles *in situ*. (B) Intramandibular muscle (Aω) cut near its insertion and reflected anterodorsally to show the insertion of the A2 adductor mandibulae muscle. Specimen BMNH 1923.7.30 : 47.

There appears to be some intraspecific variation in the shape and orientation of Aω. The smaller fish dissected has the posterior margin of the muscle (and its associated tendinous area) sloping forward to lie in about the same line as the fibres of A2. The condition of the muscle in the larger BMNH specimen is illustrated in Fig. 4.

The main body of the A2 muscle inserts onto the medial and lateral aspects of the lower jaw (Figs 3 & 4). On the medial face it inserts chiefly through three stout tendons, two of which are contiguous and parallel with one another and lie lateral to the third tendon, the lowest and largest of the three, which inserts into a shallow, ill-defined recess on the dorso-posterior aspect of the coronomeckelian bone. A fourth, smaller, tendon runs parallel with the third tendon described above; it also attaches to the coronomeckelian bone, through a small eminence immediately dorsal to the other insertions. Finally, part of A2 has a more musculose insertion lateral to those already described, but also attaching onto the dorsal margin of the coronomeckelian bone.

On the lateral face of the lower jaw (Fig. 3), A2 attaches along the entire posterolateral margin of the angulo-retroarticular, and forward onto that small area of the dentary which contributes to the coronoid process. The lateral area of A2 insertion does not extend so far forward as does that of its medial part.

Levator arcus palatini muscle. As compared with the levator arcus palatini in halosaurs and notacanths, that of *Albula* is relatively very small (Fig. 3). Its origin is narrow and confined to the sphenotic; its insertion is mainly on the hyomandibula, but with a substantial part inserted on the metapterygoid (Fig. 3).

Adductor arcus palatini muscle. No trace of this muscle can be found, presumably because of the close contact between the skull and the palatopterygoid arch (see Forey, 1973b : 159–160).

HALOSAURIDAE

Halosaurus guentheri Goode & Bean

Ligamentum primordium. This well-developed ligament runs from the posterior part of the angulo-retroarticular to the head of the maxilla (Fig. 5). Here it attaches at a point slightly behind the maxillopalatine articulation and immediately posterior to the tendon from A1β.

There is also a posterior connection between the maxilla and the dentary effected through an ill-defined ligament lying in the connective tissue of that region.

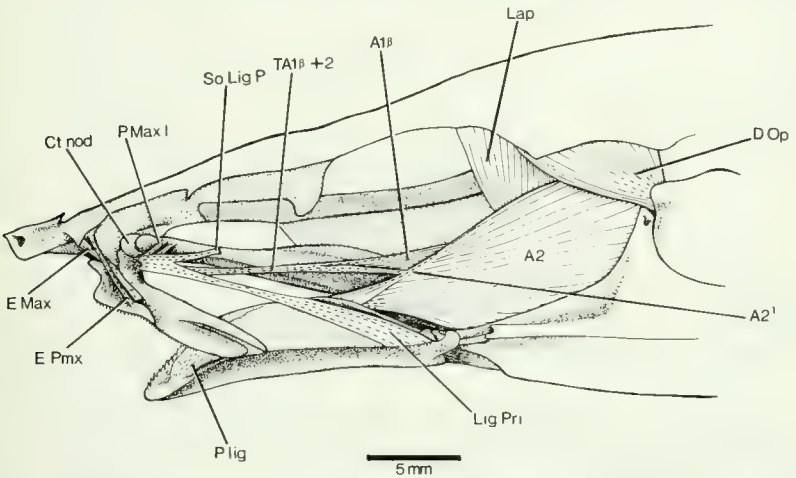

Fig. 5 *Halosaurus guentheri*. Jaw musculature and ligaments in left lateral view. Specimen BMNH 1966.10.14 : 1.

Ethmomaxillary and ethmopremaxillary ligaments (Fig. 5). A strong ethmomaxillary ligament has its origin on the lateral cornua of the ethmoid, slopes steeply backwards and downwards, and inserts onto the maxilla along its anterolateral face below the palatine process. The ethmopremaxillary ligament is of almost the same size; since its origin on the ethmoid is much deeper than that of the maxillary ligament, it crosses over the latter near its origin. It inserts dorsally onto the premaxilla about two-thirds of the way along its length.

Palatomaxillary ligaments (Fig. 5). On each side a pair of parallel and slender ligaments runs obliquely forward from the autopalatine (near its head) to insert on the maxilla at the same level as, but medial to, the ligamentum primordium.

Palatopremaxillary ligament. A stout and strong ligament is present; it inserts medially onto the inner aspect of the premaxilla.

Suborbital maxillary ligament (Fig. 5) A long, thin ligament runs from the 3rd or 4th suborbital bone partly to the head of the maxilla, where it is either contiguous with or fuses onto the anterior part of the ligamentum primordium, and partly to the sesamoid bone (or cartilage) lying between the maxilla and the palatine. Slightly anterior to the midpoint of this ligament there is a smaller, inner division which runs rostrally to insert on the ethmoid.

Adductor mandibulae muscles (Fig. 5). The main body of this complex, the adductor A2, originates on the preoperculum, the hyomandibula and, to a lesser extent, on the metapterygoid. Its insertion is along the posterior margin of the angulo-retroarticular.

On its dorsal margin, at a point about one-quarter of the distance from the insertion, there is a small, ill-defined slip of muscle which soon becomes tendinous and joins the tendon running forward from the A1β muscle (see below). Since this muscle slip is so poorly differentiated from A2, and because I find difficulty in homologizing it with any jaw muscle in other teleosts, I have called it A2^1 (Fig. 5). With regard to its possible homology, it should be noted that A2^1 does seem to show some similarity with the muscle identified as A1β in *Albula vulpes* (see p. 71). The identity of A2^1 in *Halosaurus* is further complicated by the situation in *Aldrovandia* (see p. 77), where there is a ligament extending from the coronoid process to the anterior part of the tendon from A1β. In other words, the ligament in *Aldrovandia* could be the homologue of the A2^1 tendon in *Halosaurus*. The direction in which this change took place could be either the result of a maxillo-coronoid ligament (as in *Aldrovandia*) being taken over by a muscle slip from A2 (or its precursor), or through a tendon losing its muscular association and becoming attached to the coronoid.

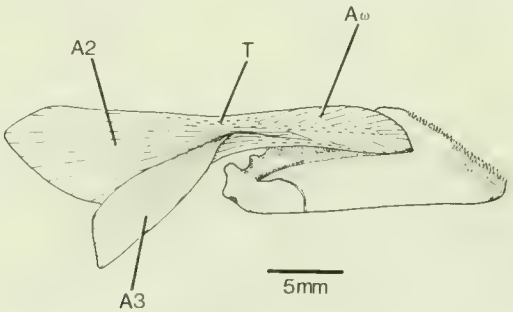

Fig. 6 *Halosaurus guentheri*. Inner aspect of left lower jaw. Specimen BMNH 1966.10.14 : 1.

Adductor A1β in *Halosaurus guentheri* (Fig. 5) is a long, slender, spindle-shaped muscle lying medial to A2 over the posterior half of its length, but dorsal to it anteriorly. The muscle has a long tendon which inserts onto the medial face of the maxilla immediately below the maxillo-palatine articulation. Posteriorly, A1β is mostly tendinous, lies lateral to the levator arcus palatini and has a flat, tendinous origin medial and slightly dorsal to that of A3 on the hyomandibula.

Adductor A3 lies medial to A1β, is a laterally compressed muscle and has an aponeurotic connection with the anterior part of A2 at about the level of the posterior margin of the angulo-retroarticular. From this aponeurosis there arises a fairly well-defined tendon which runs forward to insert on Meckel's cartilage below but touching that part of A2 which fills the entire Meckelian fossa. Within the fossa, the central part of A2 becomes tendinous, the fibres radiating out dorsally and ventrally in a distinct pinnate fashion (Fig. 6). Presumably this part of the muscle should be identified as the Aω portion of the adductor complex.

Levator arcus palatini muscle (Fig. 5). This large, top-shaped muscle has an extensive origin on the pterotic and sphenotic skull regions, and a much narrower insertion onto both the metapterygoid and the membrane spanning the gap between that bone and the hyomandibula. A small part also inserts onto the hyomandibula itself. The levator arcus palatini is not obviously subdivided, as it is in notacanthids, although the part inserting onto the hyomandibula is rather tendinous.

ADDUCTOR ARCUS PALATINI. No distinct muscle is present, but a certain amount of ligament-like thickening is visible in the posterior orbital part of the connective tissue joining the skull and palatopterygoid arch.

DILATATOR AND LEVATOR OPERCULI MUSCLES (Fig. 5) Both muscles are moderately well developed.

Halosaurus carinicauda (Alcock)

The cephalic muscles and ligaments of this species are virtually identical with those in *H. guentheri*.

Halosauropsis macrochir (Günther)

The *jaw ligaments* in this species are basically like those of *Halosaurus guentheri*, except that there does not seem to be a maxillo-suborbital ligament, and the *ligamentum primordium* has a double insertion, one part going to the maxillary head, the other to the sesamoid bone (see p. 91) intercalated between the maxilla and the articular facet on the palatine. The *ethmomaxillary* and *-premaxillary* ligaments both stem from the lateral end of the ethmoid cornua, and although the ligaments cross (near their origins), that to the premaxilla has the more lateral origin (that is, the reverse of the situation in *Halosaurus* and *Aldrovandia*). The paired *palatomaxillary* ligaments appear relatively stouter in this species than in the other halosaurids examined.

JAW AND ASSOCIATED MUSCULATURE, The jaw muscles are virtually identical in their gross morphology with those of the *Halosaurus* species examined. However, adductor $A2^1$ is greatly reduced so that its tendon joining that of $A1\beta$ arises mainly from the tendinous sheet attaching A2 to the coronoid process of the lower jaw. Also, the union between the tendons of $A2^1$ and $A1\beta$ occurs almost at the head of the maxilla and not about halfway along the tendon of $A1\beta$ as in *Halosaurus*.

The *levator arcus palatini* muscle in *Halosauropsis macrochir* has a much larger area of origin than it does in *Halosaurus*. It extends forwards along the ventral face of the frontal to wrap around the posterodorsal half of the eyeball.

The *dilatator* and *levator operculi muscles*, however, are relatively no larger than those in *Halosaurus*.

Aldrovandia gracilis Goode & Bean

JAW LIGAMENTS (Fig. 7). The *ethmomaxillary* and *ethmopremaxillary* ligaments in this species are arranged as in the *Halosaurus* species examined, as is the posteriorly broadened *ligamentum*

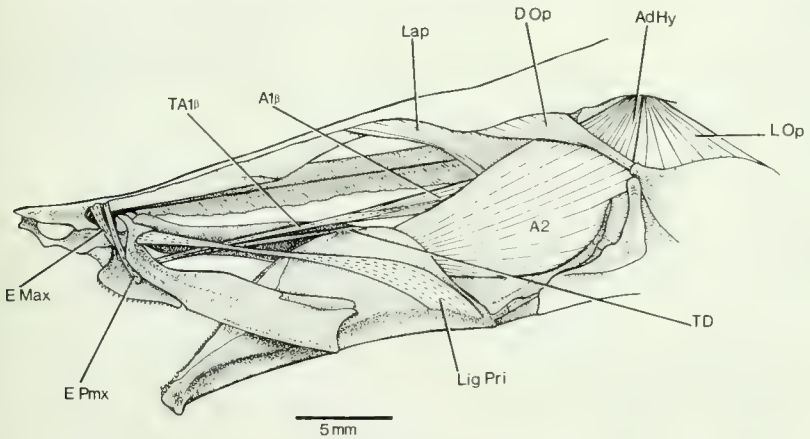

Fig. 7 *Aldrovandia gracilis*. Jaw musculature and ligaments in left lateral view. Specimen from 'Discovery' collections, station 7857, no. 5.

primordium. However, there is no maxillo-suborbital ligament; in this respect the species resembles *Halosauropsis macrochir*. The *palatopremaxillary* ligament of each side is stout and well developed, the paired *palatomaxillary* ligaments are finer and are closely applied to the sesamoid cartilage interposed between the maxillary and palatine heads.

JAW MUSCULATURE (Fig. 7). In its basic bauplan, the adductor musculature of *A. gracilis* closely resembles that in *Halosaurus* and *Halosauropsis*. The most noticeable differences are: (i) The absence of an A2[1] muscle slip from the dorsal margin of A2 (see p. 74 above). (ii) The virtual absence of a distinct A3 muscle except near its origin; distally, A3 is not readily separable from A2 and at that point the conjoined muscles are rather tendinous. The fairly extensive and musculose Aω originates aponeurotically from this area.

The *levator arcus palatini* is a well-developed muscle and has a long origin extending into the orbit; in this respect it more closely resembles the muscle in *Halosauropsis macrochir* than that in *Halosaurus*.

As in other halosaurids, no obvious *adductor arcus palatini* is present, although a few muscle fibres are present in the connective tissue joining the palatopterygoid arch with the parasphenoid.

The *dilatator operculi* muscle in *Aldrovandia gracilis* is relatively smaller and weaker than that in the other halosaurids studied, but unlike these species *A. gracilis* does have a discrete *adductor hyomandibulae* muscle.

The *levator operculi* muscle is quite comparable with that in other halosaurids.

Aldrovandia affinis (Günther)

The jaw and palatine arch musculature, the jaw ligaments and the opercular musculature are identical with those of *Aldrovandia gracilis*, and include a separate adductor hyomandibulae muscle.

Comments and comparisons

Pterothrissus belloci has a primitive system of adductor mandibulae muscles in which only the Aω (intramandibularis) muscle is differentiated from the main adductor mass.

There is no muscular control of the maxilla in this species, for although the ligamentum primordium is developed it is not associated with any muscle fibres. *Elops saurus*, whose adductor mandibulae muscles are almost as unspecialized as those of *Pterothrissus* (Vrba, 1968; Winterbottom, 1974), however, does have a few fibres from the adductor mass inserting onto the ligamentum primordium, thereby achieving some muscular control of the maxilla.

A ligamentum primordium occurs in *Amia* and is of widespread occurrence amongst teleosts. Generally, as in *Amia*, it is associated with part of the adductor muscle complex (see Winterbottom, 1974: 231–233). In some advanced teleosts this muscular encroachment results in the ligament losing its posterior connection with the lower jaw, thus becoming the tendon through which the A1 division of the adductor inserts onto the maxillary head. The absence of muscle fibres attaching to the ligament in *Pterothrissus* and *Albula* is probably a specialization and one correlated with the relative immobility of the upper jaw in those genera.

The subdivided levator arcus palatini muscle of *Pterothrissus* would also seem to be a specialized condition (and one repeated in notacanthids and lipogenyids; see pp. 79 & 83).

Albula vulpes has an undivided levator arcus palatini but like *Pterothrissus* it has no muscle fibres inserting on the ligamentum primordium (p. 71). As compared with *Pterothrissus*, its adductor muscles are more specialized. Of particular interest in this connection is the differentiation of a tendinous linkage between a dorsally located muscle slip on the main adductor and the maxillary head, quite independent of the ligamentum primordium. This connection seems to foreshadow the discrete A1β muscle found in halosaurids and can be considered a derived feature of *Albula*. It would also seem to be an actual manifestation of Dietz's (1912) hypothesized origin for A1β as a subdivision of the larger, more superficial division of the primitive adductor complex.

The adductor mass itself shows some incipient subdivision in *Albula*, at least with respect to its insertions on the lower jaw (see p. 72), although the body of the muscle remains undivided.

All the halosaurids examined share one specialized feature of the jaw musculature, a discrete A1β muscle (see pp. 73–76) lying lateral to the levator arcus palatini and inserting onto the head of the maxilla.

There is in these taxa, as compared with *Albula*, a greater differentiation of the main adductor mass, with the development of a distinct or almost completely distinct A3 division medial to A2.

In *Halosaurus* (and somewhat less obviously in *Halosauropsis*) there is a small slip of muscle originating from the main body of A2 (Fig. 5). It soon becomes tendinous and ultimately fuses with the tendon of A1β. This small muscle (A2^1; see p. 74) appears to be a specialization found only in *Halosaurus* and *Halosauropsis*. *Aldrovandia* has no trace of the muscle slip, but there is a ligament running from the top of the coronoid process to join the tendon from A1β near the latter's insertion onto the maxilla (see Fig. 7). Presumably this ligament is homologous with the tendon from A2^1 in *Halosaurus* and *Halosauropsis*. Because it is impossible to determine the direction in which the evolution of these two conditions took place (see p. 74 above), one cannot say which is specialized relative to the other. However, if it be accepted that the two conditions are homologous, then it seems reasonable to consider both as derived features of the Halosauridae.

A well-developed ligamentum primordium, without any muscular associations, is present in the halosaurids (see pp. 73, 75 & 76).

The level of adductor subdivision and specialization in the Halosauridae, especially the evolution of an A1β control of the maxilla, closely parallels that seen in certain stomiatoids, as well as in at least some myctophids, and in certain cetomimoids amongst the neoteleostean Euteleostei (see Rosen, 1973 : 412–421 for details of these latter fishes). No halosaurid, it may be noted, shows a development of the adductor arcus palatini comparable with that found in these neoteleosteans. Indeed, an adductor arcus palatini could well be described as lacking in halosaurids. No described euteleostean shows a muscle slip comparable with the A2^1 of *Halosaurus* and *Halosauropsis* (or the morphologically equivalent tendon in *Aldrovandia*), and none has a ligamentum primordium like that in the halosaurids. What similarities there are in the jaw musculature of halosaurids and neoteleosts must therefore certainly be ranked as convergence.

McDowell (1973) does not give any direct account of the jaw muscles in the Halosauridae, although he does comment elsewhere in his monograph (1973 : 130) that the pattern in *Halosaurus* is essentially like that in the various notacanthids he had examined. This comment will be discussed on p. 84 below.

II NOTACANTHIDAE and LIPOGENYIDAE

McDowell (1973 : 130) briefly describes and comments on the jaw musculature of notacanths, his remarks being based on dissections of *Notacanthus chemnitzi*, *N. sexspinis*, *N. spinosus*, *N. abbotti* and *Polyacanthonotus africanus*, as well as on Trotti's (1945) account of *N. bonapartei*. There are several points where I would disagree with McDowell's generalizations, and these are discussed below (p. 84).

NOTACANTHIDAE

Polyacanthonotus rissoanus (De Filippi & Vérany)

Maxillo-mandibular ligaments. No discrete *ligamentum primordium* can be recognized; it seems unlikely that the ligament has been taken over by one of the adductor muscles (see below). Posteriorly there is a ligamentous connection between the hind margin of the angulo-retroarticular and the medial face of the maxilla near the base of its spine.

Ethmopremaxillary and ethmomaxillary ligaments (Fig. 8). Both ligaments have a common origin almost at the tip of the ethmoid, the former ligament attaching to the premaxilla near its middle, the latter at the point where the lower limb of the maxilla curves ventrally and the spine is produced backwards.

A thick ligament runs from the ethmoid (above and posterior to the origin of the proximally united ethmomaxillary and ethmopremaxillary ligaments) both to the maxillo-palatine cartilage

and to the head of the maxilla (inserting mostly on the cartilage). This ligament would seem to be homologous with the *deep ethmomaxillary* ligament of *Notacanthus* (see p. 81).

PALATOMAXILLARY LIGAMENTS. I can find no trace of any palatomaxillary ligaments; their absence is probably to be correlated with the type of palato-ethmoid articulation found in this species; that is, indirectly through an interposed cartilaginous and connective tissue nodule and not directly between the palatine and ethmoid (see below, p. 90). A well-developed *palatopremaxillary* ligament, however, is present.

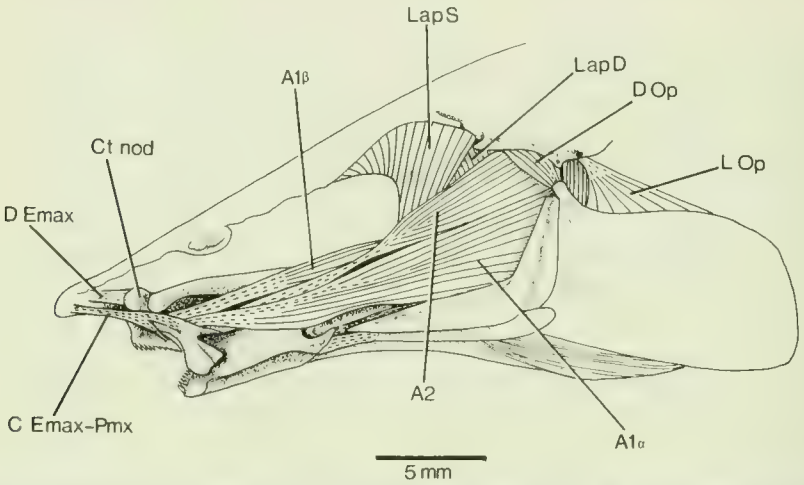

Fig. 8 *Polyacanthonotus rissoanus*. Jaw musculature and ligaments in left lateral view. The palatopremaxillary ligament has been removed to show the underlying ligaments. Specimen from 'Discovery' collections, station 8512, no. 4.

ADDUCTOR MANDIBULAE MUSCLES (Fig. 8). The largest element in this series is a ventral muscle which originates mainly on the preoperculum but with a few fibres also stemming from the pterotic. The muscle narrows anteriorly, and at about the level of the coronoid process becomes tendinous. In turn, the tendon narrows as it runs forward to insert medially on the head of the maxilla at the same level as does the ethmomaxillary ligament laterally. Posteriorly a few fibres from this muscle also insert onto the lower jaw, and there is an additional tendinous connection between the muscle and the coronoid process.

Since it inserts principally onto the maxilla the muscle should be identified as part of the A1 division of the adductor. Its lateral position in the series, and the fact that a medial A1β muscle is also developed suggests that it is a homologue of A1α in other teleost groups (see Winterbottom, 1974 : 232–233). The absence of a discrete ligamentum primordium, such as occurs in *Albula*, *Pterothrissus* and the Halosauridae, was noted above. Because in many taxa throughout the teleosts (including such primitive forms as the Elopidae) a lateral portion of the adductor musculature has enroached upon the ligament (thus gaining an insertion on the maxilla) it is possible that in *Polyacanthonotus* too the ligament has become incorporated with the adductor series. But if this is so, the ligament has lost its posterior contact with the lower jaw, which it has not done in the Elopidae (see Vrba, 1968) or in many other groups. For this reason I would argue that the maxillary insertion of A1α in *Polyacanthonotus* is not *via* a former ligamentum primordium but is an insertion created *de novo* by the encroachment of the muscle onto the bone.

Dorsal to A1α is a much smaller muscle (Fig. 8) with the outline of an isosceles triangle, and with a very elongate tendon (about twice the length of the muscle itself). It inserts onto the medial face of the dentary immediately below the last few teeth on that bone; its origin is entirely from

the pterotic region of the skull. From the tendon of this muscle there is a branch which runs medially to join the tendon from A1β (see below).

Since the principal insertion of this muscle is onto the lower jaw it would appear to be homologous with the A2 division of the adductor muscle in other teleosts, although in these fishes A2 generally lies ventral to A1 and not dorsally as it does here.

The A1β division is an elongate, rather tendinous muscle originating on the medial aspect of the hyomandibula (thus also medial to the levator arcus palatini). It inserts through a long tendon onto the medial face of the maxillary head; a few fibres also insert onto the pterygoid arch. There is a direct connection between the tendons of A1β and A2 (see above; Fig. 8); a branch from the tendon of A1β is attached to the posterior face of the dermopalatine, which is, of course, a separate and movable element of the palato-pterygoid arch in notacanthids (see McDowell, 1973 : 129).

The deepest division of the adductor series (visible only after dissection), the A3 muscle, lies medial to A1α and the ventral margin of A2 (Fig. 8). It is a narrow muscle originating from the hyomandibula, and has a long tendon running forward to insert onto the medial face of the dentary just below the insertion of the tendon from A2.

No definite Aω division can be defined, the area it would otherwise occupy in the lower jaw being filled with the tendons from A2 and A3.

The *levator arcus palatini*, a large muscle whose origin extends anteriorly into the orbit (Fig. 8), is clearly subdivided into a major, vertically aligned and deep portion (inserting mainly on the hyomandibula but with a few fibres going to the pterygoid arch as well), and a smaller, more superficial and pyramidical part which inserts only on the pterygoid arch.

As in the halosaurs no trace of an *adductor arcus palatini* could be found in *Polyacanthonotus rissoanus*.

The *dilatator operculi* is a short and small muscle (Fig. 8), the *levator operculi* is comparable with that in the halosaurids dissected.

Polyacanthonotus africanus (Gilchrist & van Bonde)

Although the adductor musculature (and jaw ligaments) of the single specimen dissected are basically like those in *P. rissoanus*, there is one important difference, namely, A2 is divided into two discrete portions.

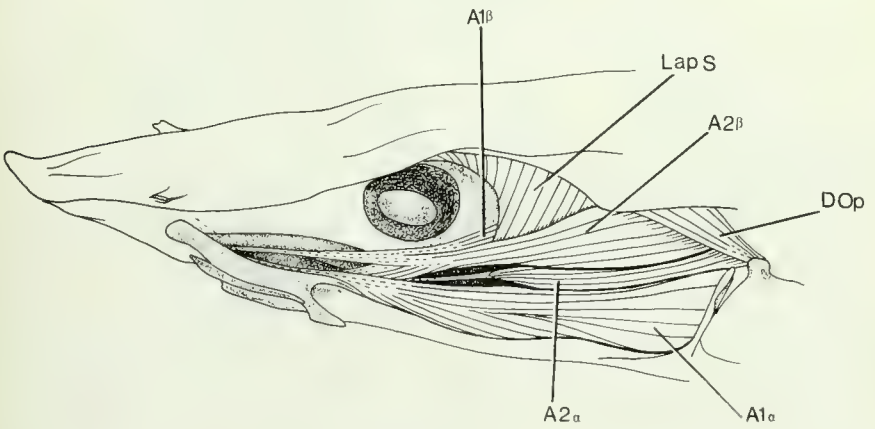

Fig. 9 *Polyacanthonotus africanus*. Jaw musculature of left side viewed obliquely from above. Specimen from 'Discovery' collections, station 8519, no. 2.

Adductors A1α and A1β in *P. africanus* (Fig. 9) have a similar form and similar relationships with the maxilla (and in the case of A1α with the dentary as well) as do these muscles in *P. rissoanus*. However, immediately dorsal to A1α there is a relatively small and short muscle (Fig. 9) whose long and slender tendon inserts onto the coronoid process of the lower jaw. In this respect it resembles the A2 division in *P. rissoanus*, although it has no tendinous linkage with A1β (see pp. 78–79). Above this muscle there is a longer and more voluminous one which, at about the level of the coronoid process, becomes partly tendinous. The upper part of the tendon fuses with the tendon of A1β; the lower part, accompanied by a few muscle fibres, inserts onto the medial face of the dentary and the angulo-retroarticular.

Since together these two muscles in *P. africanus* have the same relationships with A1α and A1β as does A2 in *P. rissoanus*, it seems likely that they represent subdivisions of that muscle; they are accordingly designated as A2α for the lower division and A2β for the upper one. In combination, A2α and β of *P. africanus* have a relatively greater volume than does the single A2 of *P. rissoanus*.

Adductor A3 in *P. africanus* is like that in *P. rissoanus* and has a broad tendinous insertion in the Meckelian fossa. No. Aω division is discernible.

The *levator arcus palatini* is similarly subdivided in the two species, but the *dilatator operculi* of *P. africanus* is somewhat longer and slightly more voluminous than that in *P. rissoanus*.

Notacanthus bonapartei Risso

Trotti (1945) has given a detailed account of the jaw muscles, and their innervation, in this species. I am in substantial agreement with Trotti's description, but since he uses a different system of muscle nomenclature for the various divisions of the adductor complex his names will be given in parentheses and prefixed 'Trotti's'.

Maxillo-mandibular ligaments. As in *Polyacanthonotus* there is no elongate and discrete *ligamentum primordium* of the halosaurid type. Also like *Polyacanthonotus* there is a dense con-

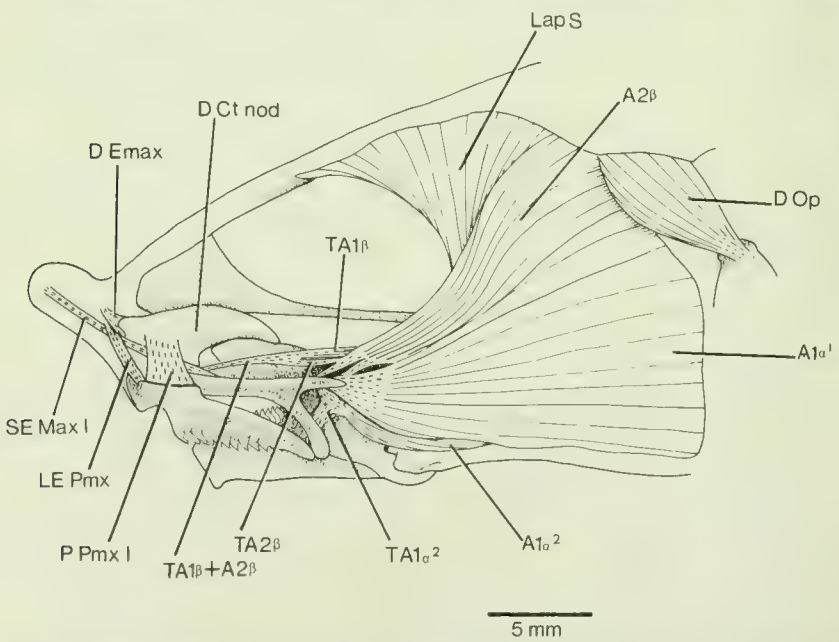

Fig. 10 *Notacanthus bonapartei*. Entire jaw musculature in left lateral view; maxillo-mandibular ligaments removed to show underlying structures. Specimen BMNH 1972.1.26 : 33.

centration of connective tissue linking the inner aspect of the posteroventral maxillary tip with the lateral face of the angulo-retroarticular.

ETHMOMAXILLARY AND ETHMOPREMAXILLARY LIGAMENTS (Fig. 10). There are two distinct ethmomaxillary ligaments. The superficial one has its origin dorsally near the tip of the ethmoid, is long and slender, and inserts on the medial face of the maxilla at about its midpoint. The deep ligament is much stouter and shorter; it runs from the head of the maxilla (where its attachment to the bone is partly obscured by the drogue-shaped maxillo-palatine nodule) to the ethmoid. Here it is attached at about the same level as the superficial ligament, but posterior to it.

There are also two *ethmopremaxillary* ligaments. A single median element connects the ascending premaxillary process to the ethmoid, while a lateral ligament (one on each side) runs from the base of the premaxillary ascending process to a point on the ethmoid near the place where the deep ethmomaxillary ligament originates. This ethmopremaxillary ligament crosses over the superficial ethmomaxillary one at about the latter's midpoint (Fig. 10).

The *palatopremaxillary* ligament is represented by a broad band of tissue extending from the lateral face of the drogue-shaped maxillo-palatine nodule to the anterodorsal margin of the premaxilla (Fig. 10).

I can find no trace of any *palatomaxillary* ligament.

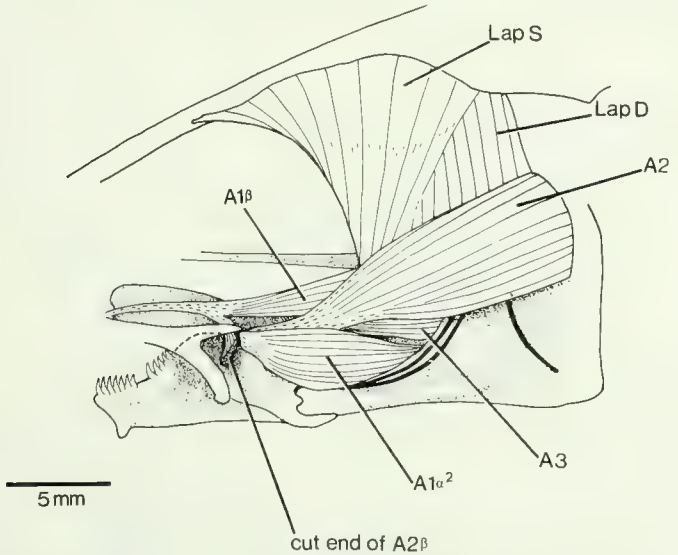

Fig. 11 *Notacanthus bonapartei.* Jaw musculature of the same specimen as shown in Fig. 10 but with the superficial muscle layers removed The tendon of adductor mandibulae A1α^2 to the lower part of the maxilla has been cut away.

ADDUCTOR MANDIBULAE MUSCLES. The largest superficial muscle in this series (Trotti's a1β) occupies a ventral position on the cheek (Fig. 10). It originates on the preoperculum and inserts through a short, broad and well-defined tendon onto the medial face of the maxilla just behind the insertion of the superficial ethmomaxillary ligament.

Immediately below the large muscle, and almost entirely covered by it, is a much smaller element (Trotti's a1α) which originates on the quadrate and metapterygoid. It has a triple insertion, firstly through a weak tendon joining that of the large muscle and thus inserting on the upper posterior part of the maxilla, secondly through a much larger and stouter tendon (at right angles to the other) inserting low down on the ventrally decurved posterior part of the maxilla (Figs 10

& 11); the third insertion is through a weak tendon onto the lateral face of the angulo-retroarticular near its summit (Fig. 11).

Although in one of the three specimens dissected there is some fibre exchange between the two muscle masses, they should be looked upon as distinct entities, especially since in the other specimens there is no exchange of fibres between them. Taken together, these muscles have the same morphological and topographical relationships with the jaws as does A1α in *Polyacanthonotus* (see above). Thus, I would identify the muscles in *Notacanthus* as subdivisions of that muscle, and would designate the larger and dorsal element as A1α^1 (Trotti's a$^1\beta$) and the small ventral part (Trotti's a1α) as A1α^2 (see Figs 10 & 11).

The large muscle dorsal to A1α^1 (Fig. 10) originates from the sphenotic and pterotic regions of the skull. It inserts through three tendons, the ventral and largest of which attaches to the dorso-posterior and medial aspect of the angulo-retroarticular. The second tendon also inserts onto the medial face of the angulo-retroarticular, but near its crown. The third and longest tendon from this muscle joins the maxillary tendon of the adductor A1β muscle at a point about halfway along its length, thus linking it, albeit indirectly, with the maxilla. At first sight this muscle would seem to be comparable with A2 in *Polyacanthonotus* (and that designated as a2 by Trotti). However, after the removal of Aα^1 and this muscle, another large muscle (originating from the hyomandibula and inserting on the lower jaw) is exposed. When, in turn, that muscle is reflected, yet another and relatively large muscle is revealed. This last element originates on the hyomandibula and partly on the metapterygoid, and would seem to be the homologue of A3 in *Polyacanthonotus rissoanus* (Figs 11 & 12). It inserts through a shared tendon onto the medial face of the angulo-retroarticular.

Thus, as compared with *P. rissoanus* there is an additional muscle in the adductor series; in other words, the situation here is like that found in *P. africanus*, namely, adductor A2 is subdi-

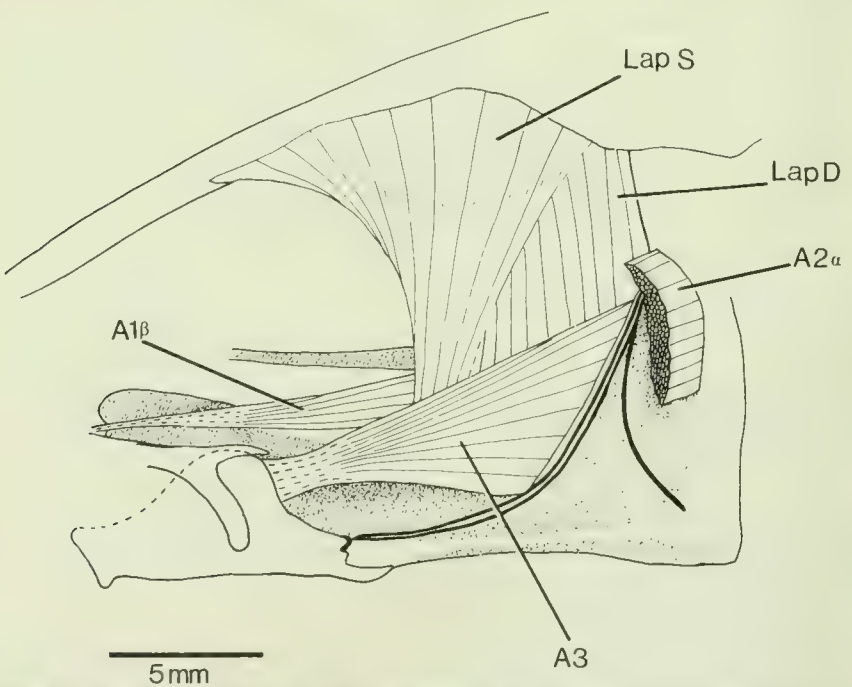

Fig. 12 *Notacanthus bonapartei*. Deep layers of the jaw musculature; same specimen as in Figs 10 & 11.

vided, its upper, and in *Notacanthus* topographically also its superficial part, having tendinous contact with the more medial A1β division as well as an insertion on the lower jaw, while its ventral and deeper division inserts only onto the lower jaw. Following the nomenclature used for *P. africanus*, the superficial muscle in *Notacanthus bonapartei* is designated A2β and the smaller, deeper division A2α. These divisions of A2 would seem to correspond respectively, with Trotti's a2 and a3 muscles (see Figs 11 & 12).

The deepest lying adductor muscle noted above (that originating on the hyomandibula and metapterygoid) should be identified as the A3 division (=Trotti's a4); see Fig. 12. It is comparable in all respects with the A3 of *Polyacanthonotus* (and, indeed, of halosaurs as well).

The A1β division (Trotti's r), like that in *Polyacanthonotus*, lies medial to the levator arcus palatini muscle and has a tendinous connection with the posterior face of the dermopalatine. It is an elongate, slender and rather tendinous muscle originating on the inner aspect of the posterior, horn-like projection on the metapterygoid, and inserting on the medial face of the maxilla near its head. According to McDowell (1973 : 130), this muscle (which he refers to as Trotti's 'Musculo R') originates on the entopterygoid, but I have not been able to confirm this in any of the specimens I have examined.

No distinct and musculose Aω division is recognizable; a short rather narrow tendon, stemming from the already tendinous distal part of A2β and running obliquely forward and downwards along the line of the suture between the dentary and the angulo-retroarticular, may represent this division of the adductor series (Fig. 13).

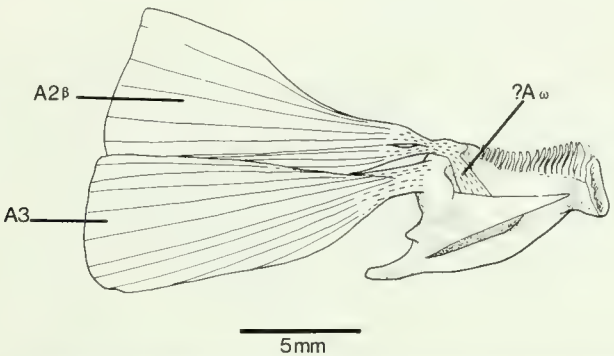

Fig. 13 *Notacanthus bonapartei*. Muscles of the lower jaw; left side, medial aspect.

McDowell (1973 : 131 footnote) describes a ligament extending from the middle of the dermopalatine to the coronoid process of the lower jaw. As far as I can tell, McDowell's ligament is the connection I have described above as the tendon stemming from the combined tendons of A2β and A1β. However, the latter attaches to the posterior face of the dermopalatine and not its middle. Despite this difference I believe that we are referring to the same element, especially since I cannot locate a ligament in addition to the tendon.

As in *Polyacanthonotus* the large and extensive *levator arcus palatini* muscle (Figs 10–12) is subdivided. The deeper part has vertically arranged fibres which insert mainly onto the hyomandibula, partly on its anterior margin but mostly onto the inner face. The smaller and superficial part is conical in shape, and has somewhat obliquely arranged fibres that insert onto the metapterygoid horn.

The *dilatator operculi* is a well-developed, deep-bellied muscle, but the *levator operculi* is thin and largely tendinous (a condition which stands in strong contrast to that in halosaurids).

No distinct *adductor arcus palatini* exists, but several groups of muscle fibres (more than in other notacanthids or in halosaurids) are present, especially anteriorly, in the connective tissue sheet spanning the gap between the skull and palatopterygoid arch.

Comments and comparisons

All the notacanthid species dissected share a number of characters, or character states, not found in the Halosauridae. The combined A1α and A1β muscular control of the maxilla is perhaps the most outstanding of these features. The absence in notacanthids of a discrete ligamentum primordium may be correlated with the development of the A1α insertion onto the maxilla; in other words, the ligament may have been taken over by the muscle, although there are arguments against this interpretation (see p. 78).

Other peculiarities of notacanthids are the subdivision of the levator arcus palatini into distinct pterygoid and hyomandibular parts (as is also the case, of course, in *Pterothrissus belloci*; p. 69), the dorsal position of adductor A2 (the mandibular muscle) relative to A1 (the maxillary muscle), the origin of A1β medial to the levator arcus palatini, and the development of a tendinous connection between A1β and the highly mobile dermopalatine.

Of these various characters, it would seem that the addition of an A1α muscular control to the maxilla, the inward shift in the origin of A1β and the development of a connection between that muscle and the dermopalatine can all be considered as derived (apomorph) features.

Indeed, the development of a combined A1α–A1β control of the maxilla is otherwise reported only in neoteleostean fishes (Rosen, 1973), particularly from amongst the Acanthopterygii (some 'beryciform' families, the sciaenids and some cottoids; Rosen, 1973 : 420). In none of these taxa, however, does the A1α division lie ventral to A2. Rosen's statement (1973 : 420) that '. . . only in Paracanthopterygii and Acanthopterygii do separate A1 and A1β occur together in the same individual . . .', must now be modified to include notacanthid elopomorphs. This similarity can only be interpreted, with respect to elomorph relationships, as convergence.

In *Polyacanthonotus africanus*, but not in *P. rissoanus*, the A2 adductor muscle is subdivided into two parts (see p. 79), a state not found in any halosaurids. However, exactly the same subdivision of this muscle occurs in *Notacanthus bonapartei* and *N. spinosus*. I would interpret this apparent synapomorphy as being a case of parallelism since there are no other characters to suggest that *Polyacanthonotus africanus* is more closely related to *Notacanthus* than to the other species of its genus. (For detailed osteological and other descriptions of the taxa involved, see McDowell, 1973.)

The subdivided A1α of *Notacanthus* (p. 82) is apparently a unique specialization; whether it occurs in all species of the genus still remains to be checked.

McDowell (1973 : 130) gives a brief and very general account of jaw muscles in notacanthids. Using Trotti's (1945) description of *N. bonapartei* as a basis for comparison, he finds an identical pattern in *N. chemnitzi*, *N. sexspinis*, *N. spinosus*, *N. abbotti* and *Polyacanthonotus africanus*. It will be obvious from what I have described above and on p. 80 that I would agree, in broad terms, with McDowell's statement so far as it concerns *P. africanus*, but that *P. rissoanus* cannot be included in this generalization. I would also agree with McDowell's further generalization that the species he examined have essentially the same pattern as in *Halosaurus* (1973 : 130), although I do not think that he has given enough prominence to the differences (mostly increased specializations in notacanthids) existing between the musculature in the two taxa. McDowell does emphasize one '. . . important and striking difference . . .', namely the increased muscular control of the upper jaw in notacanthids, especially the development of an A1α division inserting primarily on the upper jaw. In one place McDowell (1973 : 130) refers to an increase in muscular attachment to the *premaxilla* (italics mine). From my dissections I can find no direct insertion of any muscle onto that bone in any notacanthid species; the insertion is only onto the maxilla, and I presume that McDowell's statement is a *lapsus*.

LIPOGENYIDAE

Lipogenys gilli Goode & Bean

McDowell (1973 : 211–213) gives a detailed account of the jaw and associated musculature in this species, but unfortunately provides no illustrations of their complete layout. We are in general agreement in our interpretations of the rather peculiar jaw arrangement and myology of *Lipogenys*; any areas of disagreement will be obvious from the account given below.

JAW LIGAMENTS (Fig. 14). These will be described in two groups, first the ones visible without more than superficial dissection, and secondly the deeper-lying group.

There are two *ethmopremaxillary* ligaments on each side; the lower and longer is broad and thick (in fact the largest ligament of the superficial series) and attaches to the median anterior projection of the premaxilla (Fig. 14). The second ethmopremaxillary ligament is thinner and originates a little above the lower ligament; it inserts slightly posterior to that ligament on the premaxilla.

A long, thin *ethmomaxillary* ligament originates slightly above the dorsal ethmopremaxillary ligament. It inserts conjointly with the broad maxillopremaxillary ligament at about the point where the premaxilla begins to curve downwards, the combined ligaments joining the maxilla at about the middle of its upper and horizontal arm.

There is a stout, moderately long *ethmopalatine* ligament originating immediately above the ethmomaxillary ligament; it inserts on the anterodorsal aspect of the dermopalatine.

The upper ethmopremaxillary, the ethmomaxillary and the ethmopalatine ligaments all originate from a common stem on the ethmoid, and all three run parallel with one another, sloping downwards and backwards.

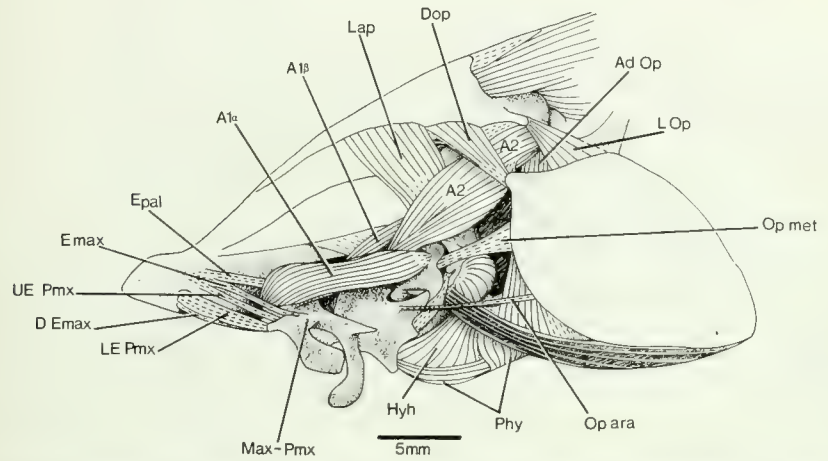

Fig. 14 *Lipogenys gilli.* Jaw muscles and ligaments in left lateral view. Specimen MCZ 38072.

There are two deep ligaments, a short, stout *ethmomaxillary* one, and a short, small and horizontally aligned ligament from the median face of the premaxilla to the dermopalatine. The deep ethmomaxillary ligament, unlike its superficial counterpart, runs upwards.

No discrete *ligamentum primordium* is present, but there is a rather diffuse condensation of ligament-like tissue in the connective tissue lying between the lower jaw and the maxilla.

In addition to those ligaments directly connected with the jaw elements there are a number of others which are involved in the mechanism of jaw movement. With two exceptions (the mandibular-opercular ligament and the posterior ceratohyal-quadrate ligament, see below), I have not been able to locate their counterparts in other notacanthoids. Presumably these neomorph structures have developed as a corollary of the profound changes in bone shape and position which characterize the jaws of *Lipogenys*.

A thin, stay-like ligament (Fig. 14) runs from the anterior border of the operculum to the angulo-retroarticular, its insertion being at a point immediately below the quadrate-articular joint. Another ligament, strong and dense, runs forward from the posteriorly directed horn of the angulo-retroarticular to insert on the quadrate immediately behind its articulatory head. A deep but thin ligament extends from the dorsal part of the anterior border of the operculum to the

posterodorsal margin of the metapterygoid; its insertion on that bone is at the same level as the origin of the A1α muscle.

The angulo-retroarticular is also linked to the posterior ceratohyal through a strong, dense, ligament which runs from the retroarticular horn to the posterior ceratohyal, inserting on that bone below and a little anterior to the insertion of the protractor hyoideus muscle. Another ligament, broad and dense, runs upwards and forward from the posterior ceratohyal to the medial face of the quadrate. (In another specimen, however, this ligament links the anterior ceratohyal with the quadrate.) The ceratohyal-quadrate ligament is probably homologous with that ligament which, in halosaurs and notacanths, links the posterior ceratohyal with the dentary (see Gosline, 1969, who also lists the occurrence of this ligament in several other groups of primitive teleosts).

ADDUCTOR MANDIBULAE MUSCLES. The most superficial element in this series, the adductor A1α (Fig. 14), is a moderately stout, elongate muscle originating from the metapterygoid, and inserting onto a distinct ledge near the head of the maxilla's lateral arm. (In *Lipogenys* the maxilla is bifurcate anteriorly; the median and shorter arm carries the articulatory head, the lateral arm is taken over almost entirely by muscle insertions and ligament attachments.) A1α is slightly thinner at its origin than at its insertion, but both points are musculose. From about the middle of the muscle there is a slender tendon closely applied to its ventral outline (Fig. 14) and which runs forward to insert laterally and slightly below the main insertion of the muscle.

Adductor A1β, the most medial of the series (not visible without dissection), is a spindle-shaped muscle originating on the spur-like process developed from the postero-dorsal angle of the metapterygoid (a site shared with a small bundle of fibres from the levator arcus palatini muscle), immediately anterior to the main body of the levator arcus palatini. Thus, in *L. gilli* A1β lies ahead of, and not lateral or medial to the levator muscle as it does in halosaurs and notacanths respectively. From its origin A1β runs forward and outwards, narrows abruptly to a fine tendon and inserts on the medial face of the maxilla.

Adductor A2, the largest muscle of the series (Fig. 14), has a complicated origin from several but contiguous centres. It is a long deep-bellied muscle that inserts, tendinously, onto the dorso-posterior part of the dentary and the angulo-retroarticular, but with part of the tendon extending onto the dorsal outline of the coronoid process as well. Its main area of origin is from the epiotic and epioccipital regions of the skull (that is, further back than in any halosaurid or notacanthid). A small, virtually separate antero-dorsal part of A2 stems from the pterotic. As the muscle runs forwards and downwards it is joined by fibres originating from the postero-dorsal part of the hyomandibula, and there is a tendinous union between A2 and the operculum near the insertion of the dilatator operculi.

The deepest adductor muscle, A3, is small and spindle shaped; it originates on the hyomandibula immediately in front of, and slightly above, the foramen for the hyomandibular branch of the 7th cranial nerve. Its insertion is on the dorsal face of the angulo-retroarticular bone.

No Aω division of the adductor series is developed.

As compared with *Notacanthus* and *Polyacanthonotus*, the *levator arcus palatini* muscle in *Lipogenys* is relatively small, though stout, and it is undivided (Fig. 14). It originates in part from the pterotic and in part from the pterosphenoid, and inserts only onto the hyomandibula.

The *dilatator* and *levator operculi* muscles, although small, are well developed and largely musculose.

There are distally distinct *adductor operculi* and *hyomandibulae* muscles in *Lipogenys*, but both share a common origin from the otic region of the skull somewhat anterior and medial to the origin of adductor A2. A few fibres from the adductor hyomandibulae insert onto the operculum.

Although not strictly part of the jaw musculature, the *protractor hyoidei* and the *hyohyoideus* muscles should be mentioned because of their prominence when the superficial musculature of the head is seen in lateral view (Fig. 14). The *protractor hyoideus* is in two parts, one of which originates from the posterior ceratohyal near its proximal head and runs, after curving ventrally and laterally, almost vertically to meet its fellow in the midline; the other part originates aponeurotically from that region where the two vertical divisions meet and runs horizontally to insert onto the medial face of the dentary (Fig. 14). The two divisions of the protractor embrace

the posterior and vertical aspects of the massive hyohyoideus muscle associated with the anterior and posterior ceratohyals. The two muscles bulge ventrally and ventrolaterally to produce the 'fat cheeks' which inspired the generic name *Lipogenys*. McDowell (1973 : 213) attributes the bulge to the hyohyoideus alone.

Comments and comparisons

Basically, the arrangement of the adductor mandibulae muscles in *Lipogenys* is like that of the notacanthids, and includes A1α and A1β muscular control of the maxilla. In particular, the muscle arrangement is nearest that found in *Polyacanthonotus rissoanus* since in this species there is no subdivision of the adductor A2 as occurs in *P. africanus* and in *Notacanthus bonapartei*.

The most noticeable differences between *Lipogenys* and the notacanthids lie in the origins of the muscles, and in an increase in the number of ligamentous connections between the jaws and the skull, including the development of ligaments not found in either the notacanths or the halosaurs. No adductor muscles originate from the preoperculum which in this genus is a flimsy ossification around the sensory canal. Instead, the muscles that should be associated with the preoperculum have all shifted their origins either to the skull (and far back on the skull too, see p. 86) or to elements of the palatopterygoid arch (see also McDowell, 1973 : 212–213). *Lipogenys* further differs from *Polyacanthonotus* in having no connection between A1α and the lower jaw. In *Notacanthus* there is no connection between the upper division of A1α and the lower jaw either, but there is one between the ventral division of the muscle and the lower jaw (see Fig. 11).

Unlike all notacanthids, *Lipogenys* has an undivided levator arcus palatini muscle (the condition found in halosaurids), and it also lacks a tendinous connection between A1β and the dermopalatine (undoubtedly a loss correlated with that bone's secondary fusion to the palatopterygoid arch, and its consequent immobility, in *Lipogenys*).

In brief, the jaw muscles of *Lipogenys gilli* (the monotypic representative of the Lipogenyidae) can be looked upon as a somewhat specialized form of those found in some *Polyacanthonotus* species (whose jaw musculature is most probably to be considered as basic for the notacanthid fishes). The muscular and ligamentous specializations of *Lipogenys gilli* are clearly correlated with the peculiar specializations of the jaws (see McDowell, 1973 : 208–214). The similarities would certainly suggest that notacanthids and lipogenyids have a shared common ancestry which is more recent than that which either family has with the halosaurs. Although the jaw musculature cannot be used to indicate a particular relationship between *Lipogenys* and *Polyacanthonotus* (because in this respect *Lipogenys* is autapomorphous and *Polyacanthonotus* is plesiomorphous for notacanthoids as a whole) there are other anatomical features which do seem to suggest that these two taxa are more closely related to one another than either is to *Notacanthus* and that a shared common ancestor can be postulated for them (see below, p. 97).

The sternohyoideus muscle in Elopomorpha

Both McDowell (1973 : 23) and Forey (1973a : 355) have commented on the relationships of the sternohyoideus muscle with the pectoral girdle in elopomorphs. Since I find myself in some disagreement with McDowell's account of the muscle in *Lipogenys* and with Forey's (1973a : 355) and McDowell's (1973) description of the situation in *Elops*, *Albula* and *Pterothrissus*, a short review of this muscle in elopomorphs would seem in order.

In *Elops saurus* much of the sternohyoideus arises aponeurotically from the hypaxial body musculature and thus lies lateral to the pectoral arch, which it covers; however, some fibres contributing to the sternohyoideus do originate from the anterior and ventral faces of the cleithrum. In contrast, the sternohyoid in *Albula vulpes* is clearly separated from the hypaxial musculature because the latter inserts onto the posterior face of the cleithrum but the sternohyoid originates mainly from its anterior and lateral faces, with a few fibres coming from the hypaxial muscles medially. The *Albula* condition is that found most commonly amongst teleosts.

In *Pterothrissus belloci* the muscle and girdle are exactly like those in *Albula vulpes*.

McDowell (1973 : 22), however, describes conditions in these two genera which are virtually the reverse of those I have found. According to McDowell (1973 : 22) for example, the situation

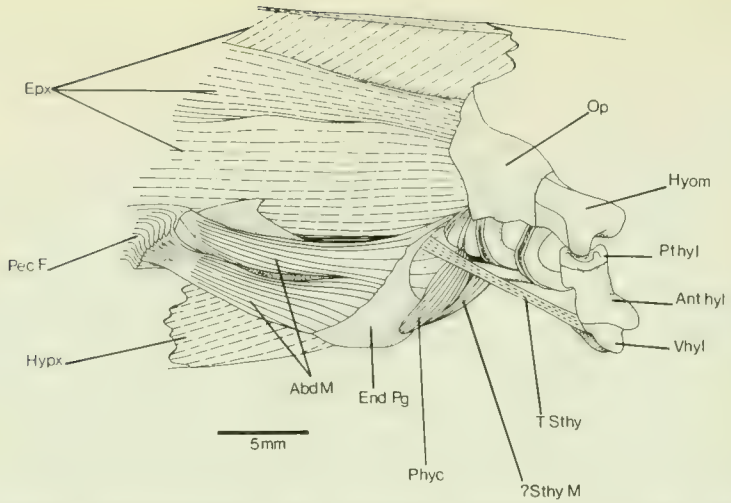

Fig. 15 *Lipogenys gilli.* Body and superficial pectoral fin muscles in the region of the sternohyoideus muscle (whose tendon, T Sthy, is visible), in right lateral view. Specimen MCZ 38072.

in *Elops* is like that I have described for *Pterothrissus* and *Albula*. Forey (1973a : 355) too describes *Pterothrissus* as having an *Elops*-like origin for the sternohyoideus.

In *Halosaurus guentheri* most of the sternohyoideus arises aponeurotically from the hypaxial muscles but a small part arises from fibres attached to the lateral face of the cleithrum's antero-ventral tip. In other words, the lateral aspect of the cleithrum is covered by muscle fibres, but none arises there (except for a few from the ventro-lateral tip). *Aldrovandia phalacra* resembles *H. guentheri* since most of the sternohyoid originates from the hypaxial musculature, and although the lateral aspects of the cleithra are covered by the sternohyoid, little of it originates on that bone. In other words, the condition in these fishes is like that in *Elops* and not that in *Albula* and *Pterothrissus*, a condition which I would consider derived rather than primitive.

The sternohyoid in *Notacanthus bonapartei* is much like that in the halosaurids examined, but in *Polyacanthonotus rissoanus* and *P. africanus* the muscle is a much longer and more discrete

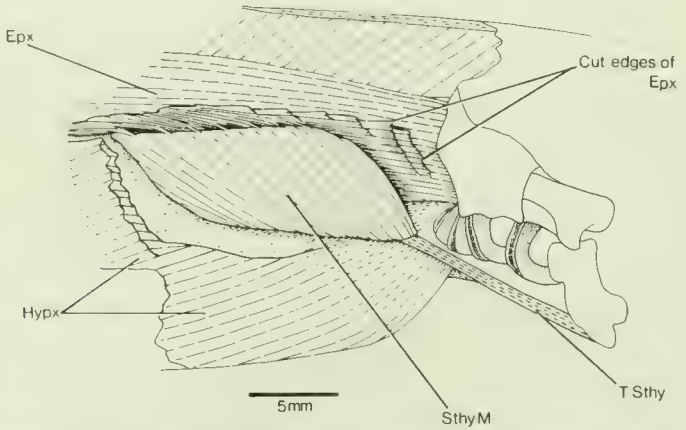

Fig. 16 *Lipogenys gilli.* Sternoyhoideus muscle. The pectoral fin musculature and pectoral girdle removed, and the superficial body musculature dissected away. Specimen MCZ 38072.

entity. It still arises aponeurotically from the hypaxial muscles but in these species its origin lies further posteriorly and its dorsal margin, for the muscle's entire length, is free from the supradjacent epaxial muscles (in *Notacanthus* and the halosaurids only a short anterior portion has a free dorsal margin).

The trend seen in *Polyacanthonotus* is carried to its limit in *Lipogenys gilli* (Figs 15 & 16). Here the sternohyoid is completely separate from the body musculature and has shifted medially so that it is now covered by superficial sheets of the hypaxial musculature. It is, in fact, invisible until these muscle sheets are removed; this doubtless led McDowell into stating that the sternohyoideus (his *rectus cervicus*) is less well developed in *Lipogenys* than in the notacanths and halosaurs (McDowell, 1973 : 220). I would agree with McDowell's correlation of the lower pectoral fin position in *Lipogenys* with the absence of a broad sternohyoideus muscle running across the lateral face of the pectoral girdle; but this is the result not, as he proposes, of sternohyoideus reduction but of its altered position. Indeed, the sternohyoid in *Lipogenys* is, relatively, a much larger muscle mass than it is in any other elopomorph fish.

The sternohyoideus of *Lipogenys* is an almond-shaped body (Fig. 16) clearly demarcated from the surrounding body musculature; it has an aponeurotic origin from the horizontal septum. From the narrow antero-ventral apex there is a stout tendon running forward to insert on the ventral face of the lower hypohyal. The tendon from the sternohyoid of each side fuses with its counterpart a little anterior to the endochondral girdle remnant; the single tendon so formed bifurcates just before the points of insertion are reached.

Two other muscles on each side are associated with the greatly reduced endochondral girdle and with the sternohyoid. A single *pharyngoclavicularis* muscle passes from the girdle to the branchial skeleton immediately behind the point where the sternohyoid tendons fuse. (As there is but one pharyngoclavicularis muscle on each side, the muscle must be considered undivided and therefore of the 'anguilliform' type; see Winterbottom, 1974 : 267.) The second muscle runs medially from the anterior face of the endochondral girdle and inserts onto the unpaired portion of the sternohyoid tendon. Since I cannot homologize this small element with any part of the musculature in this region of a more 'normal' teleost type, it is probably part of the sternohyoid. Possibly it represents the only remnant of the true sternohyoid, the larger deeper muscle then being a neomorphous feature.

Winterbottom (1974 : 266) has drawn attention to the difficulty of defining the posterior limits of the sternohyoideus when that muscle is continuous with the hypaxial musculature (as it is in most elopomorphs). He suggests that in such cases the first three myomeres of the muscle be considered as constituting the sternohyoideus. If such a definition be accepted, then virtually all of the 'sternohyoideus' in *Lipogenys* lies posterior to the third myomere and would have to be considered a neomorphous structure.

To summarize: amongst the 'herring-shaped' elopomorphs (McDowell, 1973 : 19), *Albula* and *Pterothrissus* have the usual teleost condition in which the sternohyoid originates mainly on the anterior and lateral aspects of the cleithrum, and the hypaxial muscles insert on to its posterior face. *Elops saurus*, in contrast, has much of the sternohyoideus arising aponeurotically from the body musculature and passing laterally over the cleithrum; a small part of the muscle does, however, still originate from the cleithrum. Halosaurids and notacanthids amongst the eel-shaped elopomorphs resemble *Elops*, with *Lipogenys* displaying an extreme development of the condition, in which the sternohyoid comes to lie below and free from the hypaxial body muscles.

In the few true eels (Anguilliformes) examined (*Anguilla* and *Conger*) the sternohyoid-pectoral girdle relationships are essentially of the *Elops*-halosaurid type.

The palatoquadrate arch in *Lipogenys gilli*

The palatoquadrate arch in *Lipogenys gilli* differs markedly from that in other notacanthid fishes (and halosaurids too) because of its relative inflexibility and because the dermopalatine is firmly fixed to it. The position of the dermopalatine on the arch also differs in this genus since it lies on the medial side of the arch about halfway along its length (and not ventrally and near its anterior tip as in other genera); see Figs 17–19.

McDowell's (1973 : 211) description of the general features of the arch of *L. gilli* gives a good impression of the way in which it roofs the buccal cavity and of its relative rigidity. However, I disagree with McDowell's description of the spatial relationships existing between the ento- and metapterygoid, and those between the metapterygoid and quadrate. McDowell seems to have overlooked the fact that the two former bones have different relative extensions on the lateral and medial aspects of the arch (see Fig. 17) Medially, the metapterygoid expands so that it overlies the anterior and antero-superior third of the quadrate, thereby forming the dorsal and dorsolateral roof to the posterior half of the cavity created by the left and right palatoquadrate arches. Each inner wall of this cavity is formed, posteriorly, by the quadrate, anteriorly by the ectopterygoid, and over its middle section by the ventrally directed tongue of the metapterygoid (see Fig. 17A).

On the lateral face of the arch, the metapterygoid does not extend ventrally over the quadrate; but the quadrate extends anteriorly on the *outside* of the ectopterygoid (which is just visible beneath and in front of the quadrate as a narrow keel). In other words, a greater area of ectopterygoid is visible on the medial than on the lateral aspect of the arch. The entopterygoid, on the other hand has its greater surface area exposed laterally (Fig. 17B), especially since medially the posterior part of the bone is covered by the dermopalatine (Fig. 17A).

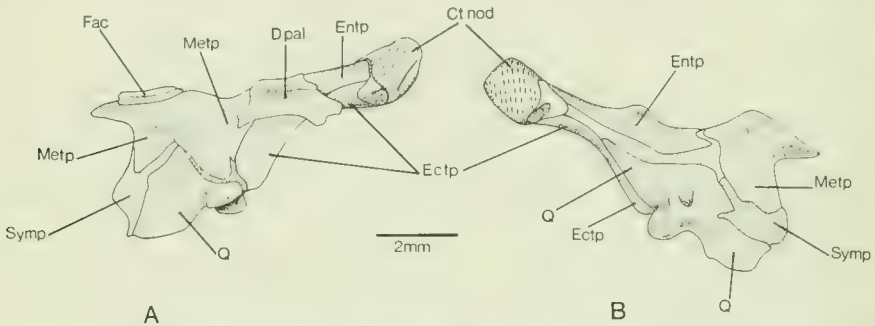

Fig. 17 *Lipogenys gilli*. Left palatoquadrate arch in (A) medial view, (B) lateral view.

Thus, I cannot agree with McDowell (1973 : 111) when he says that '. . . The largest dermal element, the entopterygoid, forms *most of the medial surface* of the palate, except at the anterior end, and is broadly spread out over the medial face of the metapterygoid and quadrate . . .' (italics mine). I would also disagree with his statement that '. . . There is a long, horizontal suture between the metapterygoid and quadrate . . .'. In my interpretation the 'suture' is the ventral outline of the metapterygoid tongue overlapping the medial aspect of the quadrate, and its alignment is more obliquely upwards than horizontally (see Fig. 17A).

In all other respects (except for the interpretation of the autopalatine, see p. 92) I would endorse McDowell's (1973 : 211) description of the arch in *Lipogenys*.

A large, cartilage-capped articular surface on the metapterygoid provides, as McDowell notes in the caption to his text fig. 4, p. 13, an articulation facet between the arch and the parasphenoid, a unique feature not found in halosaurid and notacanthid fishes.

The autopalatine problem in halosaurs and notacanths

When reviewing palatal structure and function in halosaurs, McDowell (1973 : 16) noted that '. . . the autopalatine cartilage is absent, unless it is represented by a small nubbin of cartilage between the anterior end of the pterygoid cartilage and the maxilla at the level of the maxillopremaxillary articulation'. Again, when referring to the palate in notacanths he says (1973 : 131), '. . . The autopalatine is absent as a bone, but is probably represented by the "singular nodule of

cartilage" noted by Günther. This "cartilage" (only its core is cartilaginous, and most of its bulk is formed by a thick, connective tissue sheathing) lies between the anterior-dorsal edge of the maxilla, the ventral edge of the ethmoid region anterior to the olfactory sac, and the dorsal surface of the pterygoid-dermopalatine articulation.'

I would question both the idea that the autopalatine is absent and the idea that it might be represented by either the 'singular nodule of cartilage' in notacanths or the nubbin of cartilage in halosaurs (see Figs 17–21).

The small nubbin of cartilage intercalated between the maxilla and the pterygoid arch in *Halosaurus* (Fig. 20), and its at least partially ossified counterpart in *Halosauropsis*, is present in such basal elopomorphs as *Albula*, *Elops* and *Pterothrissus*, species in which a clearly recognizable, albeit cartilaginous autopalatine is also present (Forey, 1973b). This nubbin also occurs in several non-elopomorph taxa as well (e.g. in clupeomorphs) where likewise there can be no doubt about the presence of an autopalatine element as well as the nubbin.

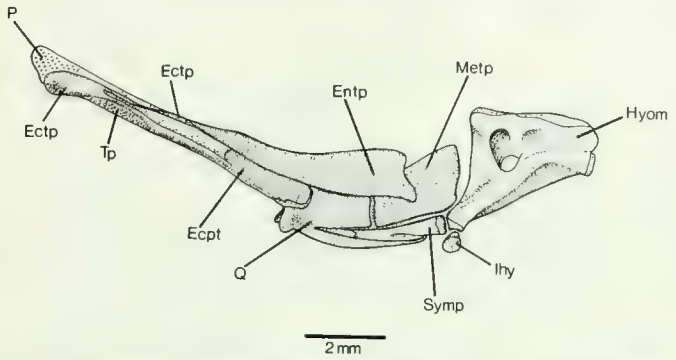

Fig. 18 *Halosaurus guentheri.* Right palatoquadrate arch, medial aspect.

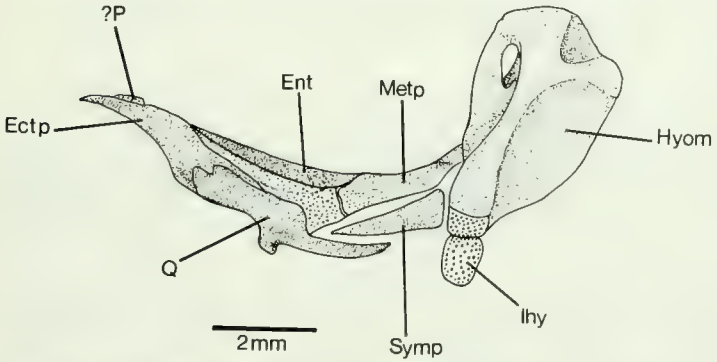

Fig. 19 *Notacanthus bonapartei.* Left palatoquadrate arch, lateral aspect.

Although I can find no trace of an ossified autopalatine in any halosaurid, I can see no reason why the cartilaginous anterior region of the palatopterygoid arch should not be identified as the autopalatine (see Fig. 18), nor why the nubbin of cartilage should not be the homologue of the similar body found in other fishes (including those elopomorphs in which an undoubted autopalatine is present; see above).

Before going on to consider the identity of Günther's 'singular nodule of cartilage' in notacanths (Günther, 1887 : 246) and its possible homology with the autopalatine as suggested by

McDowell, some attention must be given to what I take to be its homologue in halosaurs. McDowell (1973 : 16), incidentally, makes no mention of its presence in that group.

In *Halosaurus guentheri* (Fig. 20), *Halosauropsis macrochir* and *Aldrovandia gracilis* there is a moderately large, near pyramidical-shaped mass of very dense connective tissue occupying the space between the head of the maxilla (which it partly overlies when the jaws are *in situ*), the head of the pterygoid arch (i.e. the autopalatine) and the ethmoid (see Fig. 20). I can find no comparable structure in *Elops*, *Albula* or *Pterothrissus*, nor in non-elopomorph taxa.

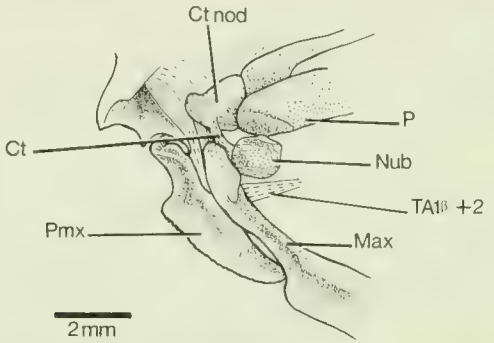

Fig. 20 *Halosaurus guentheri*. Figure to show interrelationships of ethmoid, palatine and maxillary bones (seen from left side). The maxilla and premaxilla have been displaced ventrally to show the connective tissue nodule (Ct nod) and the cartilaginous nubbin (Nub). Specimen BMNH 1966.10.14 : 1.

In *Notacanthus bonapartei*, however, there is a similar but larger structure occupying the same position between the ethmoid, maxilla and head of the pterygoid arch and actually linking the two latter elements (Fig. 21). The drogue-shaped body curves around the antero-medial surface of the pterygoid arch (which is cartilaginous at that point) and reaches to the spine-like tip of the maxillary head; a strong ligament connects the drogue with the tip of the premaxillary ascending process.

Unlike the pyramidical body in halosaurs, the drogue in *Notacanthus* has a cartilaginous centre but, as in halosaurs, its body is composed largely of dense connective tissue. I can find no cartilaginous or bony nubbin interposed between the pterygoid arch and the maxilla of *Notacanthus* and would thus suggest that it has been incorporated in the body of the drogue.

It is, I think, difficult to dispute the presumed homology of the pyramidical and drogue-shaped bodies in halosaurs and notacanths respectively. Furthermore, judging from Günther's rather small figure and from his description (Günther, 1887 : 246 & plate 10), his 'singular nodule of cartilage' is the same body as that which I am calling the drogue-shaped one, and thus is the equivalent of the pyramidical body in halosaurs.

The autopalatine in *Notacanthus* would appear to be represented by a small conical area of cartilage near the tip of the pterygoid arch (Fig. 19).

Polyacanthonotus rissoanus and *P. africanus* are much like *Notacanthus bonapartei*, but with a narrower and more elongate drogue-shaped body.

In *Lipogenys gilli* (Fig. 17) the connective tissue mass is an elongate pyriform body, its apex directed anteromedially and its base closely applied to the cartilaginous head of the pterygoid arch (which, on my interpretation, is the autopalatine); a groove in the body provides an articulatory surface for the maxilla. Embedded within the pyriform body is a fairly substantial concavo-convex nubbin of what appears to be bone (or very hard cartilage); it is this nubbin of bone which provides an articulatory surface between the pyriform body and the autopalatine. (See also McDowell, 1973 : 210–211, under autopalatine.) The embedded bony nubbin in this species represents a condition in the relationships of the nubbin (bone or cartilage) and the larger con-

nective tissue body (the 'nodule') which is intermediate between the *Halosaurus* type and that of *Notacanthus* (see above, and Figs 20 & 21). The relationships of the maxilla with the pyriform body in *Lipogenys* can also be considered as intermediate between the other two types.

Thus, contrary to the view of McDowell (1973 : 6 & 131) cited on p. 90 above, I would consider that an autopalatine is present in halosaurids, notacanthids and lipogenyids, and that the nodule of connective tissue (or connective tissue and cartilage) present near the anterior tip of the autopalatine is a neomorphous structure (probably characteristic of these three families alone) which evolved as part of the peculiar jaw mechanisms found in these fishes. That the function of the connective tissue nodule differs in notacanths (including lipogenyids) and halosaurs is perhaps indicated by its different relationships with the upper jaw and pterygoid arch in the two groups (cf. Figs 20 & 21).

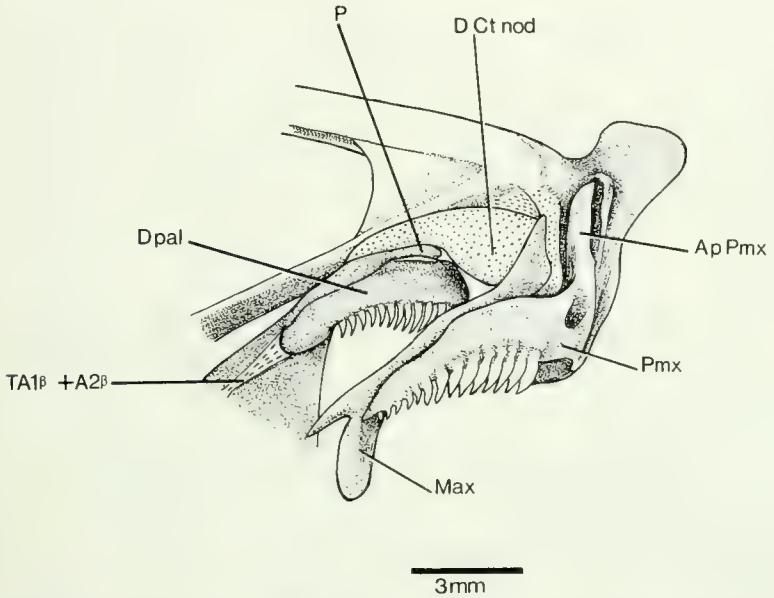

Fig. 21 *Notacanthus bonapartei.* Figure to show ethmo–palato–maxillary relationships, viewed obliquely from a ventro-anterior position (right side); the various elements are depicted *in situ.* Specimen BMNH 1972.1.26 : 33.

Since the primitive elopomorphs *Albula* and *Pterothrissus* have a double contact between the palatopterygoid arch and the skull (anteriorly with the ethmoid cartilage, and somewhat more posteriorly with the lateral ethmoid), the single contact in halosaurs and lipogenyids must be considered a derived condition, and the complete loss of direct contact in notacanths (see above, p. 92) a further specialization.

Lateral line scales

In all halosaurids, notacanthids and lipogenyids, the canal-bearing lateral line scales on the flanks are highly specialized. The sensory canal is a soft, membranous tube supported by a pair of flanges developed from the scale itself (see McDowell, 1973, for a detailed and illustrated account).

The notacanthid and lipogenyid types (McDowell, 1973 : 173 & 218 respectively) are very similar and seem to represent either a regressed or a basic state relative to those of the halosaurs.

In halosaurids (e.g. *Halosaurus guentheri*, *Aldrovandia affinis* and *Halosauropsis macrochir*) the canal scales are relatively enlarged (slightly to markedly so). But the overlap of the surrounding scales is such that the exposed area of each canal scale is not noticeably larger (and may even appear smaller) than that of its neighbours.

Notacanthids (e.g. *Notacanthus bonapartei*, *Polyacanthonotus rissoanus* and *P. africanus*) and lipogenyids, by contrast, have pore scales that are equal in size or even slightly smaller than the surrounding scales. The overlap of surrounding scales, however, is so extensive that no part of the canal scale, except for the canal, is visible; furthermore, the canal scale is very deeply embedded in the dermis. McDowell (1973 : 137) says that the canal scales are '. . . larger than the other scales of the flank . . .' but this is certainly not the case in the species I have examined (see above).

Two different types of canal scale arrangement are found in the 'herring-shaped' elopomorphs, but the canal itself is of the usual teleost type. *Elops saurus* and *Albula vulpes* have canal scales that are the same size as their flanking neighbours, and a scale arrangement whereby equal, or almost equal, areas of the canal and neighbouring scales are exposed (*Albula* has the smaller area of canal scale visible). In *Pterothrissus*, however, the canal scales are almost completely covered by their neighbours so that the canal itself and a small sector of the scale's posterior margin are visible; the canal scales are also slightly smaller than the other scales.

In other words, the spatial relationships and the relative size of the lateral line canal scales in *Pterothrissus* are very similar to those in the notacanthids and lipogenyids, and should be considered specialized relative to the condition found in *Albula* and *Elops* (and in all other elopoids as well; personal observations). The condition in *Albula* is certainly unlike that in any halosaurid or notacanthid fish.

Interrelationships and classification

In their provisional classification of teleost fishes, Greenwood *et al.* (1966) grouped in one superorder, the Elopomorpha, the albuloid, elopoid, anguilloid and halosauroid fishes. Their classification, which has formed the basis for all recent discussions, is as follows:

Superorder **ELOPOMORPHA**
  Order **ELOPIFORMES**
    Suborder **ELOPOIDEI** (families Elopidae and Megalopidae)
    Suborder **ALBULOIDEI** (family Albulidae including Pterothrissidae)
  Order **ANGUILLIFORMES**
    Suborder **ANGUILLOIDEI** (23 families)
    Suborder **SACCOPHARYNGOIDEI** (3 families)
  Order **NOTACANTHIFORMES** (families Halosauridae, Lipogenyidae and Notacanthidae).

Since 1966 there have been several important papers dealing with different aspects of elopomorph taxonomy and phylogeny, in particular with the phyletic integrity of the Elopomorpha as a whole (see Forey, 1973a, for a review; also Forey, 1973b; Nelson, 1973; McDowell, 1973 especially pp. 5–27). Intragroup relationships have been touched upon by McDowell (1973) and Nelson (1973), and have been discussed at length by Forey (1973b).

Apart from Nybelin (1971) and Gosline (1971), there seems to be a general agreement amongst those who have considered the question that the Elopomorpha do represent a monophyletic assemblage (see Forey, 1973a). None of the anatomical data discussed above would appear to contradict that conclusion, and some seem to provide new data for testing hypotheses already proposed on phyletic relationships within the superorder. Certain new hypotheses can also be generated.

Forey (1973a & b) maintains, as was inferred by Greenwood *et al.* (1966) that '. . . elopoids are more closely related to albuloids than to any other group'. However, the two synapomorph characters which Forey (1973a) believes unite these suborders, the presence of rostral ossicles and a prenasal ossicle, are in fact features which characterize all the non-anguilliform Elopomorpha, and not just the elopoids and albuloids (see McDowell, 1973 : 5–12).

In the same paper, Forey (1973a : 358, Fig. 1) gives a cladogram in which the Notacanthiformes (*sensu* Greenwood *et al.*) have a common ancestry with the Pterothrissidae, both groups ultimately having a shared common ancestor with the Albulidae. This conclusion will be reviewed

later. Forey (1973b), in his monograph on fossil and living elopiforms, provides evidence, mostly osteological, for the proposed common ancestry of the albulids and pterothrissids. As far as I can see, his arguments for this latter relationship are sound. Unfortunately neither here nor in his other paper does he provide a really critical review of his proposal that the notacanthiforms may be pterothrissid derivatives (Forey, 1973b : 214). The main features on which Forey reaches this conclusion are seemingly the elongate snout and small, inferior mouth of notacanthiforms, coupled with the restricted mobility of the upper jaw elements and the slender, inturned head of the maxilla (Forey, 1973b : 211). Certainly these are derived features shared by the two groups, but I believe that other evidence argues against their use as indicators of ancestor–descendent relationship (although not against their relationships as sister groups). Again, I would have reservations about Forey's (1973a : 355) idea that '. . . the Pterothrissidae appear particularly important in the ancestry of the halosaurs'. Some of the characters he deals with are synapomorphous ones for the Elopomorpha as a whole (sensory canals, relationship of premaxilla and maxilla, reduction in ossification), while I would interpret the association of the sternohyoideus muscle with the pectoral girdle as being like that in *Albula* and not of the halosaur type as he suggests (see above, p. 87).

Nelson (1973) has proposed alternative views on intragroup phylogenies. Using the morphology of the lower jaw as a basis for his arguments, Nelson postulates the existence of three lineages within the Elopomorpha, viz. 'elopoids', 'albuloids' (i.e. albulids, pterothrissids, notacanths and halosaurs) and 'anguilloids', the two latter groups being more closely related to one another than either is to the 'elopoids'. The characters used by Nelson provide no information on the interrelationships of the taxa within his 'albuloid' lineage. The integrity of the 'albuloids', however, is supported by the nature of the specialized rostral commissure found in all its extant representatives (see McDowell, 1973 : 5–11).

The various characters and character suites which I have dealt with in this paper lead me to agree with Nelson's concept of an albuloid group that is but distantly related to the elopoids; unfortunately these same data do not provide any evidence either to support or to reject Nelson's idea of close relationship between albuloids and anguilloids.

Returning now to Forey's (1973a & b) contention that the Pterothrissidae and Albulidae, particularly the pterothrissids, are the taxa most closely related to the Notacanthiformes we find that some of the characters discussed previously in this paper appear to support this relationship; these must be reviewed critically before they are utilized as a basis for classification.

Although the pterothrissids show a predominance of unspecialized (i.e. plesiomorph) anatomical features, particularly in the jaw and buccal musculature (see p. 76), there is one character associated with the jaw mechanism which is shared with the Notacanthidae and Lipogenyidae but with no other elopomorph groups nor with any basal non-elopomorph teleosts, namely, a levator arcus palatini muscle which is clearly subdivided into two parts (see p. 69 & Fig. 1).

A second specialization shared by pterothrissids, notacanths and lipogenyids lies in the almost complete overlap of the flank lateral line canal scales by neighbouring scales (see p. 93), with the result that only the canal and a very small sector of the scale's free margin is visible without dissection; in notacanths and lipogenyids, this overlap is complete because the canal scale lies deep in the dermis (see McDowell 1973 : 136–137 & 221–222 for detailed descriptions).

In these two features the affinities of the Pterothrissidae would certainly seem to lie with the notacanthids and lipogenyids rather than with the Albulidae and Halosauridae. Are there then any features of the Albulidae which might suggest particular affinities within the Notacanthiformes, especially with the halosaurs?

The answer to that question would seem to be negative, both from the osteological and myological evidence available. The osteological evidence (see Forey, 1973b : 202–210; and below) shows only apomorph features shared by the Pterothrissidae and Albulidae, whilst the myological evidence provides only one derived feature (the development of an A1α muscle) and that shared by albulids, halosaurids and notacanthids.

Thus, there might seem to be grounds for considering the pterothrissids to be more closely related to the notacanthids (and lipogenyids) than to the albulids or halosaurids.

However, the notacanthids, lipogenyids and halosaurids share five major derived characters

which are not present in either the Pterothrissidae or the Albulidae, viz. the presence of a spine posteriorly on the maxilla, extreme reduction of the caudal fin skeleton, the pelvic fins connected basally by a membrane, the pectoral fins set high on the body (see McDowell, 1973 : 2), and the presence of a large and characteristically shaped fibrous and sometimes partly cartilaginous nodule developed between the maxillary head and the palatine (see above, pp. 92 93).

Thus, if one were to link the Pterothrissidae with the Notacanthidae and Lipogenyidae because of their shared apomorph features of a divided levator arcus palatini muscle and the covered lateral line pore scales (see p. 95), how would the five halosaur–notacanth synapomorphies be explained?

One cannot argue that the halosaurs and notacanths had a more recent common ancestry than that shared with the pterothrissids because the halosaurs do not share with the pterothrissids and notacanths the two derived features of a divided levator arcus palatini and overlapped lateral line scales. Neither is it possible, as an alternative phylogeny, to ally as sister groups the albulids and halosaurs, on the one hand, and the pterothrissids and notacanths, on the other, since this would demand that the five halosaur–notacanth synapomorphies were evolved in parallel (and, of even greater importance, there are no synamorph features linking the albulids and halosaurids).

Finally, it must be noted that the pterothrissids and albulids share a number of derived features that do not occur amongst the halosaurids and notacanthids. These synapomorphies, according to Forey (1973b : 202–210) include a reduced intercalar bone, the nature of the ethmoid–palatine articulation, the morphology of the hyopalatine arch (including the foramen between the hyomandibula and metapterygoid bones), the spatial relationships of the hypohyals to one another and to the anterior ceratohyal, and various reductional trends in the caudal fin skeleton, including the loss of expanded bases to the inner caudal rays.

From all this evidence it would seem therefore that two sister groups can be recognized, an albulid–pterothrissid one and a halosaur–notacanthid one (the latter group including the lipogenyids, see below p. 97). Allowing for the various autapomorphic features present in each sister group, the pterothrissid–albulid pair would rank as the pleisiomorph assemblage, the halosaur–notacanth–lipogenyid group as the apomorph one.

There is one difficulty in accepting this proposed phylogeny, namely the two synapomorph features shared only by the pterothrissids and notacanths. For the moment this can only be explained as parallel evolution, probably the expression in one derived and one otherwise primitive lineage of features latent in their common ancestor. Certainly this degree of parallelism is far less extensive than that which would have to be invoked if the alternative phylogeny was proposed. In that case the albulid–pterothrissid synapomorphies as well as those shared only by notacanths and halosaurs would all have to be attributed to parallel evolution, an altogether less probable and unparsimonious explanation.

The shared common ancestry of the pterothrissids, albulids, halosaurids notacanthids and lipogenyids (the five elements also of Nelson's 'albuloids') is reflected in the specializations of their lower jaw sensory canal system (see Nelson, 1973 : 346), in the rostral portion of the infraorbital canal system (see McDowell, 1973 : 5–11), and probably also in the way in which the ligamentum primordium is either absent or is not associated with any part of the adductor mandibulae musculature. In the Elopidae, the adductor is inserted partly on this ligament; since a similar condition is found in *Amia*, this strongly suggests that the 'albuloid' condition is a derived one.

To these five taxa, all represented in the extant fauna, may be added a sixth, the extinct family Osmeroididae of Forey (1973b); various derived osteological features in that family suggest its close relationship with the Albulidae (see Forey, 1973b), and help better to define the relationship existing between the Albulidae and Pterothrissidae (see p. 35 below).

Before going on to propose a formal intragroup classification of the 'albuloids', and before considering Nelson's (1973) proposed relationships of the 'albuloids' with other elopomorph groups, one should review the inter- and intrarelationships of the halosaurs, lipogenyids and notacanths.

I can find no features which would indicate a close relationship between the Halosauridae and any particular lineage within the Notacanthidae or with the Lipogenyidae. The specialized

characters of the halosaurs are either autapomorphies, like the highly modified lateral line scales, or else merely indicative of a distant, shared ancestry with the notacanths and lipogenyids.

McDowell's (1973 : 157) view that amongst the notacanths *Polyacanthonotus* is '. . . the more halosaurid-like genus and presumably the more primitive . . .' is deceptive. What, in effect, he is saying is that *Polyacanthonotus* retains some primitive features that are lost in *Notacanthus*. *Polyacanthonotus* shares several derived features with *Notacanthus* and *Lipogenys* alone (see below). I can detect none that would suggest closer relationship with the halosaurs.

Within the notacanth group (*Polyacanthonotus*, *Notacanthus* and *Lipogenys*), *Lipogenys* is outstanding for its obvious oro-buccal specializations (see McDowell, 1973 : 208–223); its phyletic relationships with the Notacanthidae are nevertheless clear-cut.

McDowell (1973 : 223) poses the cladistically somewhat imprecise question of whether *Lipogenys* is derived from the Notacanthidae or from some pre-notacanthid ancestor retaining resemblances to the Halosauridae. His answer is equivocal. However, if the question is rephrased in terms of identifying sister groups, then I think the new information available on lipogenyids and on notacanths, combined with that already available from McDowell's work, points towards the recognition of *Polyacanthonotus* as the sister group of *Lipogenys*, the two taxa then becoming the sister group of *Notacanthus*.

Although most of the derived features seen in *Lipogenys* are autapomorphies (see McDowell, 1973 : 208–209), at least four specializations or trends in specialization are shared only with *Polyacanthonotus*, namely:

(i) There is a single lateral line scale for every three vertical scale rows on the trunk.

(ii) In *Polyacanthonotus* the endochondral shoulder girdle (scapula and coracoid) is clearly separated from the dermal girdle; in *Lipogenys* the endochondral girdle is also distinct, but in this case the entire dermal girdle has disappeared. I associate these characteristics on the grounds that the *Polyacanthonotus* condition represents a first stage in the evolution of the *Lipogenys* one. Furthermore, in both genera the scapula and coracoid ossifications of the primary girdle are well separated by a cartilaginous area; again, *Lipogenys* shows the more extreme condition.

(iii) The highly developed and well-differentiated sternohyoideus muscle in *Lipogenys* (see p. 89 and Figs 15 & 16) is foreshadowed by the large sternohyoideus of *Polyacanthonotus*, where the muscle is longer and more clearly demarcated from the body musculature than it is in *Notacanthus*.

(iv) In both genera the webbing between the pelvic fins is reduced. A fifth, and 'trend', character should probably be added to this list. In *Lipogenys* the frontal and parasphenoid are in broad contact through a deeply interdigitating suture anterior to the pterosphenoid; in *Polyacanthonotus* the frontal and parasphenoid are narrowly separated by a shallow tongue of the pterosphenoid, whereas in *Notacanthus* the bones are widely separated (see McDowell, 1973 : 12–13 & 223).

Of the five characters which McDowell (1973 : 223) lists as being shared by *Polyacanthonotus* and *Lipogenys*, three (the short ischial process of the pelvic girdle, the gradual transition between the spine-like and articulated anal rays, and the absence of scales anteroventrally on the snout) are plesiomorphic ones; the other two are derived features and were considered in the last paragraph.

McDowell (1973) also lists seven characters shared by *Lipogenys* and *Notacanthus*, which features he considers to be '. . . specializations . . . that would suggest direct derivation . . .' of *Lipogenys* from *Notacanthus*. These features are: (i) the loose attachment of the peritoneum to the body wall; (ii) the long and complexly folded intestine; (iii) A scaly branchiostegal membrane; (iv) the large number of spine-like pelvic rays; (v) the scaly sheath on all the sensory canals of the head; (vi) the very strong angulation of the maxilla; (vii) the shape of the scales.

I find it difficult to assess the significance of the peritoneal character, but since it does not occur elsewhere amongst the Elopomorpha it is presumably a derived one.

The intestine in *Polyacanthonotus africanus* and in *P. rissoanus* is elongate and folded, so the condition in *Lipogenys* could be interpreted as a further development of a trend already apparent in a common ancestor.

The question of whether or not a scaled branchiostegal membrane is an indicator of a *Lipogenys–Notacanthus* relationship is complicated by the fact that some individuals (or perhaps populations) of at least one *Polyacanthonotus* species do have scales on the branchiostegal mem-

brane. A specimen of *P. rissoanus* (BMNH 1904.3.4 : 3) from South Africa has numerous, but scattered, small and very superficial scales over the entire area of the branchiostegal membrane. No scales can be detected on another specimen of this species (N.I.O. 'Discovery' collection, Stn 8512) nor on two specimens of *P. africanus* (N.I.O. 'Discovery' collection, Stns 7853 & 8519) although in the larger of the two latter fishes there are marks on the membrane very similar to those left when scales are rubbed off from the scaled *P. rissoanus*. Whether the apparent nakedness of the branchiostegal membrane in many *Polyacanthonotus* is due to the abrasion of these small and superficial scales or whether scaled specimens are individual or population variants remains to be tested on larger samples than are available to me. Whatever the answer, it does seem that this feature cannot be used to indicate a closer relationship between *Lipogenys* and *Notacanthus* than between *Polyacanthonotus* and *Lipogenys*.

Two of the four other characters from McDowell's list, in my opinion, also fail to demonstrate any such relationships. Some species of *Polyacanthonotus* have two spine-like rays in the pelvic fin, that is the same number as occurs in *Lipogenys* and *Notacanthus*; the peculiar, apparently serrate second pelvic spine in *Lipogenys* (see McDowell, 1973 : 221) is certainly an autapomorphic character. In all specimens of *Polyacanthonotus* which I have examined the sensory canals of the head are scale-ensheathed except for the medial region of the rostral commissure; in having this canal region scaled *Lipogenys* does resemble *Notacanthus*, but again it is difficult to decide whether this is the primitive or derived condition (but see below). The maxilla in *Polyacanthonotus* is distinctly angled although not quite so strongly angled as in *Notacanthus*, but the difference between the three genera is one of only slight degree; the greater similarity existing between *Notacanthus* and *Lipogenys* in this feature could well be attributed to functional convergence. Finally, there is the question of scale shape. Again I must disagree with McDowell. As Fig. 22 shows, the scales of *Polyacanthonotus africanus* have a near vertical anterior margin, and clearly demarcated dorsal and ventral margins, in these respects differing from the scales of *Notacanthus bonapartei* but closely resembling those of *Lipogenys*. There is some topographically correlated variation in scale shape in any individual of *Polyacanthonotus*, but nowhere on the body could I find scales that were more like those of *Notacanthus* than those of *Lipogenys*.

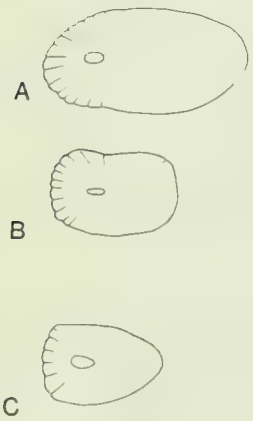

Fig. 22 Body scales from (A) *Notacanthus bonapartei*, (B) *Lipogenys gilli*, (C) *Polyacanthonotus africanus*.

In brief, only two of the supposedly *Notacanthus*-like features listed by McDowell (1973 : 223) seem to be shared uniquely by *Lipogenys* and *Notacanthus*, namely, the loose peritoneum and the absence of scales on the rostral commissure. The former is probably a derived feature since it does not occur in the primitive, that is elopoid, Elopomorpha, but the latter character may be primitive because this region of the snout is naked in halosaurs, pterothrissids and albulids, all taxa which are manifestly more primitive than the notacanthids.

If this analysis be accepted, then there is little to support the relationship implicit in McDowell's (1973 : 223) suggestion of *Lipogenys* having '. . . direct derivation . . .' from *Notacanthus*. On the contrary, I would submit that the actual specializations as well as the trends of specialization shared by *Lipogenys* and *Polyacanthonotus* suggest a common ancestry for the two taxa and that *Notacanthus* represents their sister lineage.

The different lineages of Nelson's 'albuloid' group can now be brought together as shown in the accompanying cladogram (Fig. 23).

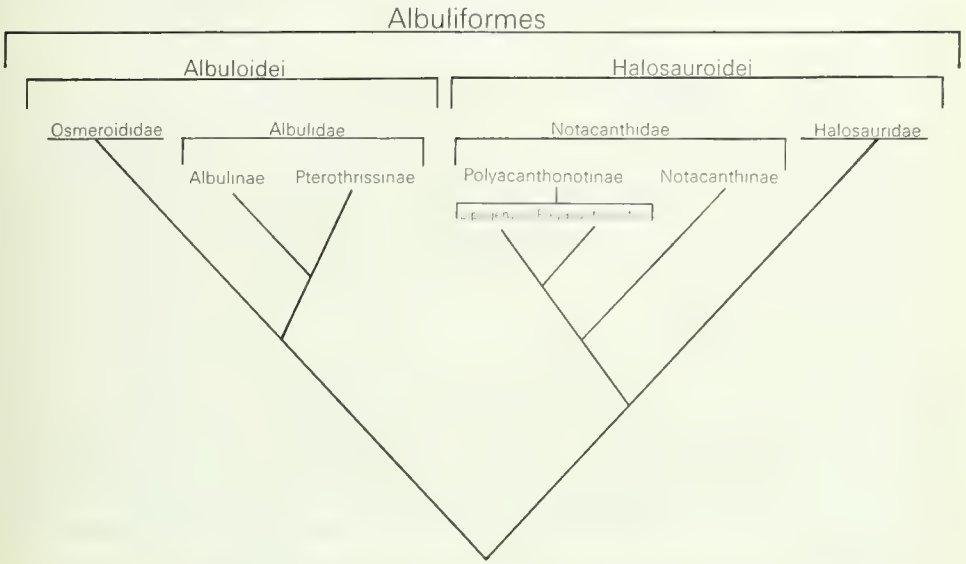

Fig. 23 Cladogram to show interrelationships of the various taxa comprising the order Albuliformes.

As this figure indicates, the overall classification agrees with Nelson's (1973) concept of an order Albuliformes; its two constituent sister lineages are given subordinal status as the suborders Albuloidei (plesiomorph) and Halosauroidei (apomorph). This arrangement differs substantially from that proposed by Greenwood *et al.* in 1966, where the Albuloidei were treated as the apomorph sister group of the Elopoidei (the two taxa constituting the order Elopiformes). In that classification the Halosauridae, Lipogenyidae and Notacanthidae were treated, without further grouping, as the constituent taxa of the order Notacanthiformes, whose relationships within the Elopomorpha could not be determined at that time.

The new arrangement also departs from Forey's (1973a) groupings which are essentially those of Greenwood *et al.* (1966). My reasons for rejecting that arrangement have been detailed above (p. 95).

McDowell's (1973) recognition of two suborders (Notacanthoidei and Halosauroidei) within a single order Heteromi (=Notacanthiformes of Greenwood *et al.*) is essentially a phenetic classification based on degrees of morphological difference, and would presumably have been the same had he taken into account the morphological differences existing between the Heteromi and the Albulidae and Pterothrissidae.

In other recent classifications (McAllister, 1968; Gosline, 1971) the albuloids have also been classified with the elopoids (*Elops* and *Megalops*) and not with the notacanths and halosaurs, an arrangement which, as will be apparent from this paper and from Nelson's (1973) research on jaw structure, is not thought to reflect phyletic relationships.

My arrangement of taxa within the Albuloidei is based largely on Forey's (1973b) detailed and meticulous study of fossil Osmeroididae, Pterothrissidae and Albulidae, combined with personal observations on the soft anatomy of *Pterothrissus* and *Albula*. It differs from Forey's treatment of the Albuloidei only in ranking the species of *Albula* and *Pterothrissus* as members of two subfamilies rather than representing two families, a change in status which I believe better represents their phyletic relationships.

Reasons for interrelating the constituent taxa of the Halosauroidei as shown in the cladogram (Fig. 23) are given on pp. 95–98 above. No further comment seems necessary if it be accepted that the categories in a classification should show propinquity of descent rather than emphasize phenetic dissimilarities, as does McDowell's(1973) recognition of the two suborders Halosauroidei and Notacanthoidei.

On the grounds of their shared specializations in swimbladder morphology (see Marshall, 1962; Greenwood *et al.*, 1966) and lower jaw structure (the angular fused with both the articular and retroarticular in *Pterothrissus* and all eels), Nelson (1973 : 348) suggested a sister group relationship between the Albuliformes (as here demarcated) and the Anguilliformes of Greenwood *et al.* (1966). As Nelson points out (1973 : 347), the fusion of the angular with both articular bones is '. . . at best a parallelism and a weak indicator of relationship.' The detailed similarities in swimbladder specializations (for which see Marshall, 1962), however, would seem to be a strong indicator of common ancestry. None of the characters dealt with in this paper weakens this hypothesis, and consequently Nelson's recognition of the Anguilliformes and Albuliformes as sister groups is accepted.

No information additional to that given by Nelson is available on the relationship between the elopiform fishes (that is, the Elopoidei of Greenwood *et al.* (1966) and Forey (1973b)) and the Albuliformes and Anguilliformes. Thus, I would also accept provisionally Nelson's (1973 : 346–348) suggestion that the Elopiformes be treated as the plesiomorph sister group of the Albuliformes and Anguilliformes combined. The plesiomorph status of the Elopiformes is clearly demonstrated by Forey's (1973b) work on both fossil and living representatives; Forey's conclusions about the intragroup relationships of these fishes are also accepted.

To summarize, I propose that the affinities of the various taxa discussed above be expressed in the following way:

Cohort: **TAENIOPAEDIA**
  Superorder: **ELOPOMORPHA** (*sensu* Nelson, 1973)
    Order: **ELOPIFORMES** (*sensu* Nelson 1973)
      Suborder: **ELOPOIDEI**
  Superorder: **ANGUILLOMORPHA** (Nelson, 1973)
    Order: **ALBULIFORMES** (Nelson, 1973)
      Suborder: **ALBULOIDEI**
        Family: **Osmeroididae** (Forey, 1973b)
        Family: **Albulidae**
          Subfamily: **Albulinae**
          Subfamily: **Pterothrissinae**
      Suborder: **HALOSAUROIDEI**
        Family: **Halosauridae**
        Family: **Notacanthidae**
          Subfamily: **Notacanthinae**
          Subfamily: **Polyacanthonotinae**
            Tribe: **Polyacanthonotini**
            Tribe: **Lipogenyini**
    Order: **ANGUILLIFORMES**
      Suborder: **ANGUILLOIDEI** (*sensu* Greenwood *et al.*, 1966)
      Suborder: **SACCOPHARYNGOIDEI** (*sensu* Greenwood *et al.*, 1966)

In an article published whilst this paper was in press, Patterson & Rosen (1977) put forward a revised interpretation of relationships within the neopterygian fishes. The section dealing with elomorph fishes in their new classification differs from that given above because Patterson & Rosen (1977 : 160, footnote) do not accept the validity of Nelson's (1973) dichotomy between

the Elopomorpha and Anguillomorpha. Instead, they treat the cohort Elopomorpha (=Taeniopaedia above) as an unresolved trichotomy comprising the orders Elopiformes, Megalopiformes (new) and Anguilliformes, the latter with two suborders, the Anguilloidei and Albuloidei. (Patterson & Rosen do not discuss the interrelationships and ranking of taxa within the two suborders.)

Following the classification proposed by Patterson & Rosen (1973: 153 & 163) my suborders Albuloidei and Halosauroidei would have to be ranked as the superfamilies Albuloidea and Halosauroidea, but the other categories would remain unchanged (except, of course, for a downgrading to superfamilies of the Anguilloidei and Saccopharyngoidei).

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Synopsis

The development of the general concept of the characters of the genus *Tremogasterina* is discussed, and a summary of the character correlations now considered to be typical of the genus is given. The astogeny of the colony, and the ontogeny of the umbonuloid frontal shield and secondary calcified orifice is described, together with observations of the ontogeny and astogeny of the avicularia and brood chambers (ovicells). Analysis of populations indicates that two divergent trends in zooid and colony structure may

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have been evolved since the Paleocene. Fifteen nominal species or populations are described, from the Paleocene to the Recent, and their distribution in time and space is discussed. Two new species are described. The nomenclature and affinities of the genus are discussed. The nature of the frontal shield ontogeny raises problems in recognition and interpretation, particularly of fossil specimens; further fields of work are suggested which may provide some solutions.

Introduction

The concept of the genus '*Tremogasterina*' has been well defined from Recent and late Tertiary fossil specimens and its characters are distinct. Unfortunately, there are problems both in the interpretation of the type-species, and in the priority of the name itself. The history of *Tremogasterina*, and of the related genus *Poricella*, is discussed on p. 125. Setting aside the nomenclatural problems, the name *Tremogasterina* is used here for a group of species having umbonuloid frontal shield ontogeny, frontal foramina, large secondary calcified orifices with oral spines, interzooidal brood chambers ('hyperstomial ovicells', see p. 124), and both interzoodial and vicarious avicularia, with mandibles slung on a complete bar or from paired condyles.

Powell & Cook (1967) showed that the characteristic foramina in the calcified frontal shield, from which the generic name was derived, could be reduced or even completely occluded during ontogeny, but that a foramen was present at least during the early ontogenetic stages. The present study illustrates the considerable morphological diversity resulting from different developmental series of one basic type of frontal shield ontogeny within the complex of species nominally assigned to *Tremogasterina*.

The anasciform affinities of *Tremogasterina* have resulted in its having been regarded as belonging to the Anasca (Bassler, 1953) and to the Ascophora Imperfecta (Harmer, 1957). Several of the forms included by Harmer in the 'Ascophora Imperfecta' do not have umbonuloid frontal shield development, and the two concepts are not necessarily the same. In the Petraliidae, Petraliellidae and Celleporariidae, for example, the ontogeny of the frontal shield shows similarities with both the cryptocystidean and umbonuloid types of development. The probability of other forms of ontogeny also requires further investigation. In fact, the number of species which have been studied in detail is so small that the assumption that a few major systematic divisions may be made on these grounds alone is almost certainly premature. On the other hand, the known differences in developmental episodes, and in their sequence, and the differences in the homology and morphology of the layers involved are apparently so important that it seems equally certain that they reflect the evolution of polyphyletic groups. The similarity in appearance among the late ontogenetic stages indicates a considerable degree of convergence and parallel development among the major groups now included in the Cheilostomata (see also p. 123).

The existence of at least two distinct methods of formation of a calcified frontal shield and related hydrostatic apparatus in some Cheilostomata has now been demonstrated in some detail (see Banta, 1970, 1971; Cook, 1973). Studies of living species and the application of hard/soft sectioning techniques have shown that although the later ontogenetic stages may appear very similar, there is a series of fundamental and correlated differences between the two methods of frontal shield calcification and hydrostatic apparatus formation.

In cryptocystidean growth the calcified layer is an interior partition wall and develops before the operculum is differentiated completely. It grows distally into a coelomic space until the primary calcified orifice is delineated. A sacciform ascus, which comprises the hydrostatic apparatus, is then formed by invagination from a group of cells proliferating from the proximal edge of the operculum. In the late stages of ontogeny, the calcified internal wall has no coelomic space on its basal side in the majority of species examined. A cryptocystidean frontal shield which remains surrounded by coelome basally and frontally is, however, known in *Tropidozoum* (see Cook, 1975).

In umbonuloid growth a frontal fold grows in a distal direction, frontally, above a previously formed anasciform frontal membrane. The operculum and parietal muscles are differentiated at an early stage in the ontogeny of the fold. The fold is calcified on its basal side only, leaving a space basally, between the fold and the frontal membrane. On the upper, frontal side of the calcified layer of the fold, there is a hypostegal coelome which communicates with the visceral

coelome by means of marginal frontal septulae. The calcified layer eventually forms a secondary calcified orifice in apposition to, but above, the uncalcified primary orifice and operculum. The space between the frontal membrane and the calcified frontal shield forms the hydrostatic apparatus, and is functionally identical with the cryptocystidean ascus. Morphologically, however, it is similar to the epistegal space of the Cribrimorpha, and this term is used here, in order to emphasize the differences between the two forms of development.

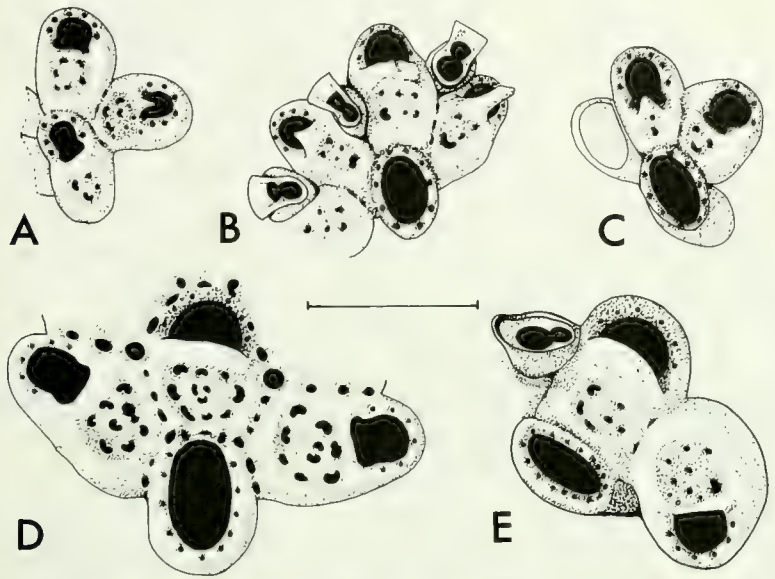

Fig. 1 Ancestrulae and primary zooids of *Tremogasterina*. Sketches showing orifices, spine-bases and frontal foramina; details sometimes based on more than one specimen. (A) *T. perplexa* Cook, Ghana, BMNH, 1973.3.22.27. Ancestrula probably missing, zooids on left damaged. (B) *T. spathulata* (Canu & Bassler), East Indies, BMNH, 1961.10.30.8.9. Note prominent apertural bar and distally descending orifice of distal primary zooid. Avicularia have been budded between primary and secondary zooids. (Spine-bases from another specimen.) (C) *T. oranensis* (Waters), Senegal, BMNH, 1970.8.10.9A (with *Membranipora arborescens*). Note large orifice of primary distal zooid; zooid on left has not developed normally. (D) *T. robusta* (Hincks), Red Sea, BMNH, 1965.8.8.8. Note large size, coalescence of areolae to form funnels, and apertural bar and distally descending orifice of primary distal zooid. (Spine-bases from another specimen.) (E) *T. mucronata* (Smitt), Gulf of Mexico, BMNH, 1961.11.2.41. Note apertural bar and distally descending orifice of primary distal zooid. (Avicularium from another specimen.) Scale = 0·50 mm.

Abbreviations and terminology

Length of zooid	Lz	Width of zooid	lz
Length of orifice	Lo	Width of orifice	lo
Length of brood chamber	Lov	Width of brood chamber	lov
Length of rostrum of interzooidal avicularium	Lr	Length of rostrum of vicarious avicularium	Lvic

BMNH	British Museum (Natural History) Collections
USNM	United States National Museum Collections
NMV	Naturhistorischen Museum, Vienna Collections
UCB	Université Claude Bernard, Lyon Collections
USC	University of Southern California Collections
MAC	Musée Royale de l'Afrique centrale, Tervuren Collections
UMC	Universitetets Zoologiske Museum, Copenhagen Collections

BROOD CHAMBER – the chamber in which the embryo is brooded. In *Tremogasterina* the chamber is exterior and has calcified walls and the term is equivalent to 'ovicell'. In many other cheilostomes the brood chamber is a diverticulum from the exterior, housed within the zooid walls, and may or may not have calcified walls.

EPISTEGAL SPACE – the space between the uncalcified frontal wall and the basal side of the frontal shield in umbonuloid and cribrimorph cheilostomes.

FRONTAL SHIELD – the cheilostome frontal wall with calcified skeleton – formed by an interior partition wall in cryptocystidean groups, by an external, basally calcified fold in umbonuloid groups, and by a series of external, calcified spinous processes in cribrimorph groups.

PRIMARY ORIFICE – the cheilostome orifice which is protected by the operculum – calcified in cryptocystidean forms, uncalcified in umbonuloid forms.

Astogeny

The early colony development is known in *Tremogasterina robusta*, *T. spathulata*, *T. oranensis*, *T. mucronata* and *T. perplexa*. In the first four species the ancestrula is membraniporiform, in the last it may perhaps be similar to succeeding zooids.

The ancestrula and early budding of *T. robusta* was described by Powell & Cook (1967). Specimens (BMNH, 1965.2.4.11, 1965.8.8.8., Massawa, Red Sea underneath oyster scutes) have from ten to eighteen long spines overarching the ancestrular opesia, and two to three primary zooid buds. The buds have six spine bases and eight to eleven frontal foramina. The ancestrula of *T. spathulata* was described by Harmer (1957 : 658). Specimens (BMNH, 1961.10.30.8 and 9, East Indies, Siboga Coll.) have ten spines and three distal zooid buds. The buds have six spines and four to six frontal foramina. Interzooidal avicularia arise between both the first and second generation zooids. The ancestrulae of *T. oranensis* (BMNH, 1970.8.10.9B, Senegal, on shell with *Membranipora arborescens* and many other species) are larger than the subsequent zooids and have a well-developed proximal gymnocyst, eight to ten spines and two to three distal or lateral and distal buds. The buds have four to six spines and two to four frontal foramina. The ancestrula of *T. mucronata* (BMNH, 1961.11.2.41, Campeche Bank, Gulf of Mexico) has sixteen spines and two primary buds. The buds have six spines and five to ten frontal foramina. Another colony, from which the ancestrula is missing, has a small, proximally orientated avicularium between the primary buds; the mandible is rounded, not truncate and distally expanded as in succeeding avicularia. The primary zooid of the colony of *T. perplexa* (BMNH, 1973.3.22.27, Ghana) is slightly damaged and may not in fact be the ancestrula. It is smaller than the next two distal zooids and has a calcified orifice with approximately six spines; there are four frontal foramina. The distal zooids have six spines and four to nine frontal foramina.

In all cases the primary buds are produced distally or distal-laterally. In several species the central distal bud in particular, has a larger secondary calcified orifice than the other zooids. The orifice descends rapidly distally, and there is a prominent suboral apertural bar, similar to that of many cribrimorphs, and to the zooids of *T. maçonnica* (see pp. 121, 128).

The primary buds, and to a lesser extent the zooids in the primary zone of astogenetic change of all species, are strikingly similar in appearance (see Fig. 1A–E). All have a distinct, slightly depressed frontal area with several small lunate or irregular frontal foramina which are not occluded by subsequent calcification. Both foramina and oral spines tend to be more numerous than in zooids in the zone of astogenetic repetition.

The majority of Recent and fossil species encrusts shell (frequently oyster shell), coral, Bryozoa and calcareous concretions. *T. mucronata*, *T. celleporoides* and *T. robusta* tend to form erect, unilaminar or occasionally loosely bilaminar and tubular expansions, arising from an encrusting base. *T. maçonnica*, *T. areolata*, *T. spathulata*, *T. perplexa* and *T. musaica* are entirely encrusting and form far smaller colonies. *T. oranensis* and *T. brancoensis* are primarily encrusting, but become erect with long tubular branches later in their astogeny. *T. brancoensis* also develops truly bilaminar branches. In nearly all species the primary zone of astogenetic repetition is followed by one or more secondary zones of overgrowth. These overgrowths arise from a focus of one or two

zooids, and grow in all directions. In *T. celleporoides*, *T. oranensis* and *T. brancoensis*, several sequential overgrowths occur, and one or more distinct growing edges may be seen to form the erect branches or lobes.

Generally, it appears that umbonuloid forms do not produce multilaminate colonies by colony-wide frontal budding, as described for some cryptocystidean forms such as those studied by Banta (1972). The presence of a hypostegal coelome in umbonuloid species makes it hypothetically possible for frontal buds to be produced, and in *Tremogasterina* the primary zooids initiating overgrowth do develop in this way. They are apparently derived from frontal septulae, which are covered by cuticle and epidermis. In thin-section it can be seen that the basal walls of the overgrowth zooids are frequently not in contact with the frontal shields of the overgrown zooids. The primary frontal bud forming an overgrowth develops later in the astogeny, but in a similar manner to the interzooidal avicularia. It is derived from the frontal septulae of adjacent zooids and in some specimens (e.g. *T. celleporoides* BMNH, 1961.10.30.16, see Pl. 1A and *T. mucronata* BMNH, 1911.10.1.1698) a row of marginal funnels (common to both zooids at this ontogenetic stage) can be seen to open into the basal side of the bud. In another specimen of *T. mucronata* (BMNH, 1931.5.2.6) there is a group of several deformed frontal buds. They arise interzooidally above the space separating adjacent zooids and extend vertically above the surface of the colony. Development was not complete at death, and these zooids may never have been able to develop normally. They are calcified on the distal (normally basal) side, and have a membranous wall on the proximal (normally frontal) side. These colonies also have dimorphic zooids (see p. 131), and may have been reacting to some unknown microenvironmental influence.

The normal frontal bud produces a triad of distal and distal-lateral zooids, in a similar pattern to that produced by the ancestrula (seen in *T. spathulata*, BMNH, 1965.9.4.1, Red Sea and many colonies of *T. oranensis*). Overgrowths later bud in all directions, and the erect, tubular branches of *T. oranensis* and *T. celleporoides* are frequently formed of several layers, some growing proximally, others laterally and distally.

Zooids of overgrowth zones are sometimes affected by microenvironmental influences especially at the earlier stages, and may be irregular in shape, but generally there appears to be little or no difference between them and the zooids of the primary zone of repetition.

Ontogeny of zooid walls

The frontal calcified shield and hydrostatic apparatus

As in other umbonuloid forms observed (see Cook, 1967, 1973), the ontogenetic changes appear to occur as a series of rapid episodes, alternating with periods of slower development. Colonies showing complete ontogenetic series are therefore rare, but zooids observed from several colonies from the same sample will usually provide information enabling all the developmental episodes to be traced. Equally complete series have not been available in all the species examined, but the ontogeny appears to follow the same general pattern (see Figs 2, 3).

Zooids at the growing edge nearing their full length possess calcified basal and lateral walls, and a partially calcified distal transverse wall at least. Uncalcified buds extending distally to partially calcified zooids do not occur very often, and suggest that, as in *Exechonella*, budding occurs in distinct episodes, rather than the continuous process found in, for example, *Membranipora membranacea* (see Lutaud, 1961). Distal and lateral septulae are present in the calcified walls and the frontal wall is entirely membranous. It is considered here that the lateral and distal walls do not develop further, i.e. that there is no further potential surface of direct contact among visceral coelomes of zooids in a primary zone of change or repetition after this stage in the ontogeny. Upward (i.e. frontal) growth from this stage may appear to be a continuation of the lateral and distal walls, and to be indistinguishable, using a light microscope, from that which preceded it, but is here regarded as frontal wall development. Additional contact among zooids is therefore entirely among hypostegal coelomes.

The calcification proceeds as a continuous, curved lamina which extends from the proximal to the distal end of the zooid. The lamina begins to turn inward, the most rapid development being

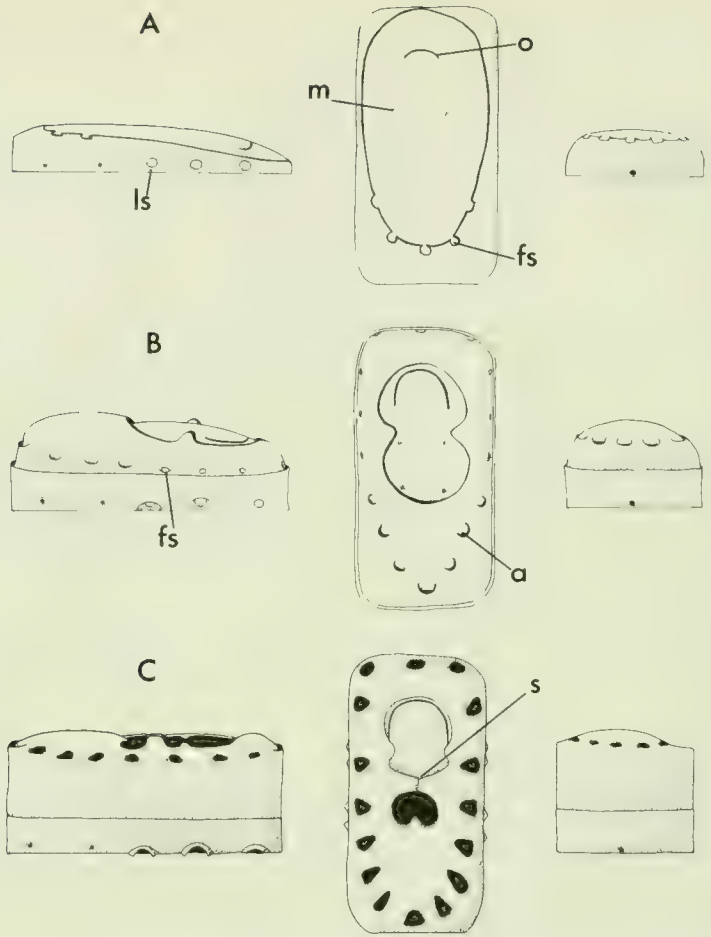

Fig. 2 Early ontogeny of the vertical and frontal walls in *Tremogasterina*. From left to right, diagrams are of lateral, frontal and proximal views of a zooid (see also Fig. 3). (A) Establishment of general basal extent of zooid by lateral calcified vertical walls. Note lateral septulae (*l s*) and incipient frontal septulae (*f s*). Differentiation of the operculum (*o*) and parietal muscles (*m*) has commenced. (B) Overarching of uncalcified frontal wall by umbonuloid fold over epistegal space. Note that thickening of calcification has already produced 'areolae' (*a*) above the proximal frontal septulae. Note that much of the upper part of the 'distal wall' is formed by the incurved transverse frontal fold. Primary (uncalcified) orifice is complete, secondary calcified orifice not yet formed. Lateral septulae developing overarching buttresses of calcification. (C) Early stage of secondary calcified orifice and foramen. Note sutures between processes forming apertural bar above opening of epistegal space. Lateral indentations of orifice are frontal to developing condyles. Note thickening of calcification and complete areolae. Lateral septulae now surrounded by chambers.

proximally and laterally. At the same time a series of multiporous frontal septulae are developed, which usually extend from the proximal to the distal end of the zooid (see Pl. 1A). A ridge of calcification develops just below the septulae, perhaps indicating the division between the lateral and distal transverse walls, and the frontal lamina. Studies on, for example, the ultrastructure of the walls may show further evidence of changes in crystal structures at this point. At this stage the uncalcified frontal wall shows the beginning of the differentiation of the operculum (see Fig. 2A). The calcified lamina above the ridge may be regarded as the basal part of a double-layered expansion, the upper (frontal) part of which is uncalcified. The double-layered expansion evaginates above the primary uncalcified wall which then can be regarded as the equivalent of an anasciform frontal membrane, including the operculum and developing parietal muscles. As calcification proceeds and both layers overarch the frontal membrane, they leave an epistegal space on their basal side (Cook, 1973, and Fig. 2B, C). It is inferred that the upper layer of the shield consists of an expansion of cuticle and epidermis above a hypostegal coelome which is in contact with the visceral coelome through the frontal septulae (see Fig. 2B). Both layers continue to develop in an umbonuloid manner above the frontal membrane, in which the operculum and frontal parietal muscles are completely differentiated.

The operculum is very thick and closely apposed, but not attached, to the secondary calcified orifice which is delineated by the anastomosis of paired distal processes in the calcified lamina (see Fig. 2C). This development is similar to that seen in *Triporula* and *Exechonella*, and in the Adeonidae (see Cook, 1967, 1973).

The development of the secondary calcified orifice is accompanied by thickening of the frontal calcification and the obscuring of the frontal marginal septulae by intervening calcified buttresses which extend upward into the hypostegal coelome. The buttresses close frontally, forming tubes in the calcification which open into the hypostegal coelome frontally, and are in contact with the frontal septulae and therefore with the visceral coelome basally (see p. 110). These tubes are 'areolae' (see Banta, 1973), and may develop further (see p. 111).

The primary frontal foramen is formed at the same time as the secondary orifice by the anastomosis of the lateral distal calcified processes (see Fig. 2C). It is usually subdivided by extension and fusion of further processes into three to four smaller foramina. These may become further subdivided by unilateral processes which project into the cavities, making them lunate or reniform. These processes themselves may bear spinules. The larger foramina may remain open, but in many cases, cuticle extends across them basally and frontally, making them uncalcified 'windows' continuous internally with the hypostegal coelome. Subsequent calcification may thicken the frontal shield considerably, and occlude or obscure the foramina (see below, pp. 111, 135), and the secondary orifice may become depressed. The area proximal to the orifice frequently becomes mucronate (see Fig. 3 and Pl. 6E). In many fossil and Recent specimens the mucro is broken or worn; the extent of growth possible is shown by specimens of *T. mucronata* collected by divers *in situ* from a submarine cliff face at 60 metres depth off northern Jamaica. The mucros of these colonies reach 0·25 mm in length and are bifid or trifid; they may be uncalcified terminally and were covered by thick cuticle. In *T. perplexa* (see p. 138) the entire frontal may develop a prominent, hollow median keel, which obscures the frontal foramina (see Pl. 1E). Conversely, the central part of the shield may not be thickened, and the foramina then become depressed in a distinct area. This occurs in *T. mucronata*, *T. celleporoides* and *T. areolata* (see also Osburn, 1950 : 98, and Pl. 1C).

The form and eventual extent of thickening is closely connected to the development of interzooidal and extrazooidal intercommunication of hypostegal coelomes (see p. 111). It is a resultant of the multivariate effects of ontogenetic age, astogenetic position, microenvironmental and environmental factors and the genetic structure of the colony.

Zooidal communications

All zooids communicate through multiporous septulae in the distal and lateral walls. Species of *Tremogasterina* are frequently stated to possess diatellae (pore chambers), and in some colonies (notably of *T. celleporoides* and *T. robusta*) they certainly appear to be present (see also Powell &

Cook, 1967). Further examination of specimens, however, has shown that there are several problems involved in the determination of diatellae which require further investigation. Recent work by Banta (1969), Gordon (1971) and Harmelin (1973) has emphasized the need to study the complete ontogeny of intercommunication structures, not just the end product. Gordon remarked (1971 : 460), 'Distinctions betweeen diatellae exist in different groups, especially in their mode of formation.' Some of the diatellae mentioned by Gordon differed in the calcification sequences. In *Fenestrulina* the outer and inner (pore plate) walls of the diatellae calcified 'more or less simultaneously', whereas in *Callopora*, as described by Silén (1944) and in *Crassimarginatella* as described by Harmelin (1973), the inner pore plate wall calcified after the outer wall. In both examples, the formation of the diatellae took place within the primary sequence of zooidal calcification. In *Tremogasterina* the formation of the outer wall of the chamber takes place, if at all, far later in the ontogeny. Multiporous septulae are formed as the lateral and distal transverse walls calcify. The next generation of zooid buds is then formed as an expansion of cuticle, epidermis and coelomic tissue from the pore plate of the septulae. It is only after the partial calcification of the zooidal walls of this bud that the formation of a calcified chamber surrounding the parent septula may occur as a distinct episode. In many colonies, and in zooids within colonies, no chamber is formed, the extra calcification being confined to intervening buttresses between septulae, especially those in the lateral walls. Generally, the distal septulae become surrounded by a distinct chamber, but in most specimens the 'pore' which leads into the distal zooid remains very large. In the *T. spathulata* group the pore may become a horizontal slit, and this development sometimes occurs in *T. oranensis*. The differences among diatellae, and between them and 'buttressed' or 'chambered' pores (see Cook, 1964 : 16), may thus be alternately interpreted as fundamental differences in ontogenetic sequence, or as stages in the evolution of distinct and complex structures (see also Harmelin, 1973 : 478 *et seq.*). The end products of these developmental series may appear to be identical, but if there are any real differences, these can only be recognized when a complete ontogenetic series is present. It seems that the term 'diatella' or 'pore chamber' should be used with caution until the ontogeny of a far greater range of species has been investigated (see also p. 124).

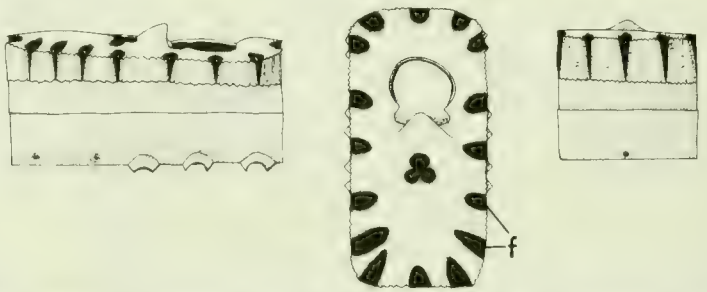

Fig. 3 Late ontogeny of vertical and frontal walls in *Tremogasterina*. (Sequence of diagrams as in Fig. 2.) Development of extrazooidal thickening and enlargement and coalescence of areolae to form funnels (f) between adjacent zooids. Note suboral mucro and further development of chambers around lateral septulae.

Both distal transverse and lateral walls are in fact very shallow, and the distal transverse wall may consist of little more then the area surrounding the distal septula. The remaining, more frontal, part of the apparent distal wall consists of the slightly inturned, distal part of the frontal umbonuloid fold. This explains the presence of cuticle traces between zooids seen in longitudinal sections. Thickening is so rapid that in frontal view, and in some sections, the calcified part of the fold may appear continuous with the distal transverse wall. In a pair of sequentially budded zooids the tubes in the calcification forming the areolae derived from the distal frontal septulae of the proximal zooid, and those from the proximal frontal septulae of the distal zooid usually

combine their cavities during thickening to form a single marginal 'funnel' in frontal view. In some colonies this occurs early in ontogeny. Similarly, the lateral frontal areolae from lateral septulae of adjacent zooids form joint funnels, as noted by Osburn (1950 : 98). The development of the brood chamber is closely related to the resultant continuity of hypostegal coelomes of both sequential and adjacent zooids (see p. 114). The coelomic connection beneath the cuticle and epidermis during later stages of ontogeny results, in some colonies, in extrazooidal thickening of the calcification in which zooidal contributions merge and become colony-wide (see also Cheetham, 1968 : 11, and Fig. 3). The transfer of nutrients to the hypostegal coelome by the frontal septulae make them the potential site of interzooidal avicularia, brood chambers and frontal buds. In *T. spathulata*, incipient frontal avicularia also arise from frontal foramina which, in this species, are closed by cuticle basally and frontally (see p. 109). The laterally placed frontal septulae are large and the calcified funnels surrounding them persistent in late ontogeny, in most species, both fossil and Recent. In the *T. spathulata* group, however, they are extremely small, and it may be possible that this is correlated both with the number and nature of the frontal foramina. In ontogenetic thickening of the calcification, these foramina themselves develop as calcified funnels which extend until they are in contact with each other and then thicken frontally forming 'blocks'. The formation of blocks of calcification is particularly well developed in *T. musaica* (see Pl. 1F), and greatly resembles that found in the later ontogenetic stages of *Exechonella*, which also has minute frontal septulae. In the *T. spathulata* group the foramina are 'windows', and are closed basally and frontally by cuticle. They are thus in contact with the hypostegal coelome directly. Due to their large numbers and extent they effectively increase the thickening of the whole frontal calcified wall. In other species, where the foramina are reduced in number, or remain open, thickening is produced by the whole frontal epidermis supplied by nutrients through the frontal septulae.

Oral spines and oral condyles

Spines are present in nearly all species and develop as small invaginations and anastomoses in the distal part of the calcified lamina of the frontal fold as it overarches the operculum. They therefore develop fairly late in the ontogeny (see p. 122). Generally, the bases of the spines are cuticular. Spine-base scars are often obscured by later calcification, but may remain distinct (see Pls 1C, F and 5B, E). Condyles develop as shallow, basally directed grooves in the lamina at the sides of the secondary calcified orifice. The inner edges of the grooves thicken and form the lateral indentations visible frontally in many specimens. Further, secondary, basally directed extensions of the calcification below the lateral indentations form the inner condyles, which are often not visible frontally. In some specimens condyles are not apparently formed. When present, they extend and insert below the lateral edges of the operculum, on the proximal side of its transverse mid-line when open, so that it becomes pivoted between the two sets of calcified processes on each side. It must be remembered that the operculum is capable of opening, and the zooid of feeding, before the completion of the frontal calcified shield in umbonuloid forms (see Cook, 1973 : 249). The condyles and lateral indentations presumably ensure that the operculum remains closely apposed beneath the thickening calcification of the secondary orifice. The occlusor muscles are very large and are inserted into the distal half of the operculum. They run vertically and slightly distally to the condyles and are inserted into the distal wall and distal part of the lateral walls near their bases. The divaricator muscles are attached to the proximal part of the operculum and are inserted in the upper part of the lateral walls.

Ontogeny and astogeny of the avicularia

Avicularia arise variously, in some species early in zooidal ontogeny. For example, in *T. mucronata* and *T. oranensis* avicularia are budded regularly between zooids, forming alternating series laterally (see Pl. 6 and 7C), and development begins as soon as the zooid frontal shields have calcified. In *T. celleporoides* position and orientation of avicularia are usually much more variable,

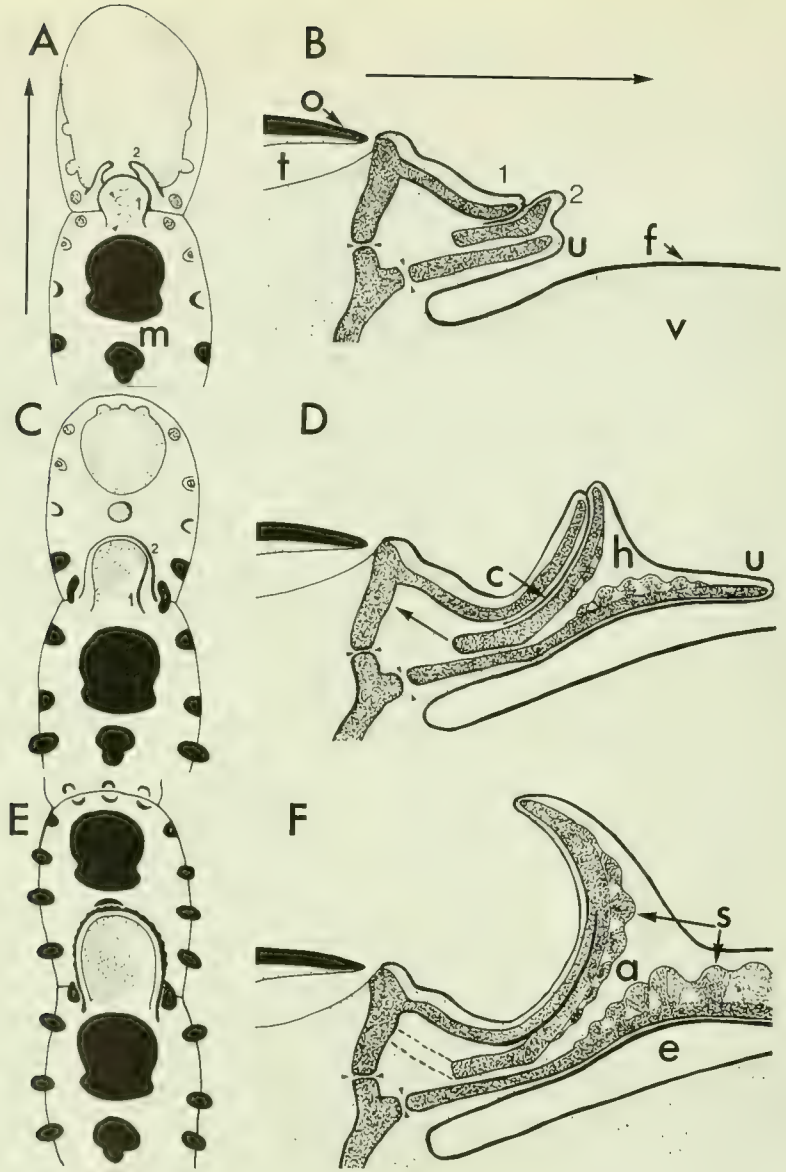

Fig. 4 Ontogeny of brood chamber. A, C, E, diagrammatic sketches of frontal appearance of brood chamber development. Cuticle omitted, direction of colony growth arrowed. D, B, F, diagrams of longitudinal sections through developing brood chamber at comparable stages; not to the same scale as A, C, F. Cuticle black, coelome light stipple, calcification dark stipple. Direction of colony growth arrowed. Distal frontal septulae of maternal zooid and proximal frontal septulae of distal zooid indicated by small arrows.

(A) Maternal zooid (*m*) with small distal lamina (1) growing distally into common hypostegal coelome expansion between maternal zooid and distal zooid (surrounded by cuticle in life). Frontal fold of distal zooid has developed crescentic outer brood chamber lamina (2) in the same way. (B) Longi-

and development does not begin until two or three zooid rows have developed fully. The subrostral chamber first appears to develop from extensions of the buttresses between areolae and as a calcified funnel, covered by cuticle. The bud derives from two or more zooids and is thus interzooidal. The rostrum and calcified bar or condyles grow beneath the cuticle, in which the mandible is differentiated in a similar manner to that of the zooidal operculum. Mandibles may be slung on a complete calcified bar, or from paired condyles; there is a good deal of intraspecific variation among populations, and even among colonies in this character. In fossil specimens, the bar is often broken and appears as paired condyles.

Mandibles and rostra also show intraspecific variation, particularly within the *T. mucronata*-complex and in *T. spathulata*. In addition the shape of the rostrum in fossil specimens may be altered by preservation or wear. The character of mandible shape is, however, fairly specific; for example in *T. robusta* mandibles are usually asymmetrical, and in *T. musaica* small and acute. In *T. lanceolata* the elongation of the mandibles is such that it apparently restricts the development of the calcified frontal shield of the next distal zooid (see also Powell & Cook, 1967). The *lanceolata*-form of growth also occurs, however, in some colonies of *T. mucronata* and *T. robusta*, particularly where the zooids and avicularia are budded in lateral rows, like the zooids of *Electra verticillata*. 'Verticillate' growth also occurs in some colonies or parts of colonies of *T. celleporoides*, but here the rounded shape of the mandibles precludes any *lanceolata*-form of frontal wall development. 'Verticillate' growth is often found in erect, unilaminar or tubular portions of colonies, but may also occur in encrusting expanses; the avicularia are almost without exception orientated distally in these colonies. Orientation of mandibles is also conspicuously distal in some species (e.g. *T. robusta* and *T. oranensis*), and lateral or random in others (e.g. *T. spathulata* and *T. celleporoides*). Nevertheless, there is also a great deal of intraspecific variation in populations of *T. spathulata* and *T. mucronata*, and in *T. brancoensis* there is a correlated change in mandible shape and orientation which is related to the geographical distribution of the populations (see p. 134). Interzooidal avicularia occur very early in the astogeny of *T. spathulata* and *T. mucronata*, arising between the first or the first and second generation zooids (see Fig. 1). In *T. robusta* and *T. oranensis* they have not been found to occur before the third and fourth zooid generations.

Vicarious avicularia are known in most species and arise among the zooids, communicating with them through lateral and distal septulae. They are a feature of overgrowth layers, often occurring in groups. In most species the rostra and mandibles are similar to those of the interzooidal avicularia, but in *T. brancoensis* they are dissimilar in the two forms. In *T. mucronata*, some colonies have dimorphic zooids, closely similar to vicarious avicularia, but with frontal foramina (see p. 131).

The frequency of occurrence of both interzooidal and vicarious avicularia varies considerably among the species. For example, the proportion of interzooidal avicularia to zooids in *T. brancoensis* is 3 : 2, in *T. areolata*, *T. mucronata*, *T. subspatulata*, *T. robusta*, *T. celleporoides* and *T. oranensis* it is approximately 1 : 1, in *T. spathulata* and *T. musaica* it is 1 : 2, and avicularia are

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tudinal section at a slightly later stage than (A), after fusion of the horns of the crescentic lamina (2), frontal to the calcified part of the developing umbonuloid fold (*u*) of the distal zooid, from which it is derived. (1) lamina from maternal zooid, (*o*) operculum of maternal zooid, (*t*) cavity of tentacle sheath of maternal zooid, (*f*) cuticular frontal wall (frontal membrane) of distal zooid, (*v*) visceral coelome of distal zooid. (C) Further development of both laminae. Note proximally directed extension of distally derived lamina (2) to meet distal part of maternal zooid frontal fold. (D) Longitudinal section at same stage as (C). Direction of proximal extension of lamina (2) which is out of section, arrowed. Note imminent fusion of two laminae terminally and the 'pinching out' of the coelomic cavity between them, leaving a cuticle trace (*c*). (*h*) hypostegal coelome, (*u*) distally migrating edge of umbonuloid fold of distal zooid. (E) Brood chamber after fusion of laminae and further frontally directed growth. (F) Longitudinal section at same stage as (E). Secondary calcification developing on outer surface of brood chamber (cf. Pl. 8C), and on frontal shield of distal zooid (*s*), (*a*) areola leading to frontal septula, (*e*) epistegal space of distal zooid. Position of proximal extension of lamina (2), which is out of section, indicated by dotted lines.

absent in *T. perplexa*. Vicarious avicularia are common in *T. celleporoides* and some populations of *T. brancoensis*. They are frequent in some colonies of *T. spathulata* and *T. oranensis*, rare in *T. robusta*, and apparently absent in *T. perplexa*, *T. musaica* and *T. lanceolata*.

Ontogeny and astogeny of brood chambers (ovicells)

The development of brood chambers varies in sequence of episodes and in the relative rate and timing of sequences both within and among colonies and species. It has been traced by observation of growing regions of colonies, including examination of thin-sections and by scanning electron microscopy. Specimens of two species, *T. mucronata* (BMNH, 1931.5.2.6) and *T. celleporoides* (BMNH, 1890.3.24.34 and 1961.10.30.16), have shown almost complete sequences of development, and the following reconstruction of the ontogeny is based upon them. Isolated episodes have been seen in colonies of these and other species which allow the inference that the process is fundamentally the same throughout the genus.

Two basic factors in understanding the ontogeny are the contact among zooids of hypostegal coelomes across the colony surface, and the rapid and continuous thickening of the frontal shield calcification which occurs simultaneously with brood chamber development. Episodes in the ontogeny are illustrated in Pl. 2 and Fig. 4.

Brood chambers are usually developed near the growing edge, but may not begin to develop until a later stage in colony astogeny. None can develop until the zooid which will produce the ovum (the 'maternal zooid', see Cook, in press) has the primary frontal shield development complete, and the next sequential, distally placed zooid or zooids have at least the proximal part of their frontal shield or shields calcified and their frontal septulae formed.

The first sign of development visible in untreated specimens is a small, flattened expansion of cuticle on the descending part of the frontal shield of the maternal zooid, distal to the newly formed secondary calcified orifice. This is an expansion of the frontal cuticle and it surrounds a small calcified lamina, which grows into the hypostegal coelome. This coelomic expansion is in contact with the visceral coelome through the areolae and distal frontal septulae. Almost simultaneously, a second, crescentic lamina develops from the proximal part of the frontal shield of the next distal zooid. This, too, is surrounded by cuticle and by hypostegal coelome which is in contact with the visceral coelome of the distal zooid through its most proximal septulae. These are just visible, but are beginning to become sunk in calcification to form areolae. Like the avicularian subrostral chamber, this lamina appears to be a modification of the buttresses of calcification which alternate with the frontal septulae and grow upward into the hypostegal coelome (see pp. 109, 112). The second lamina thus grows upward into the expanded hypostegal coelome as a pair of crescentic, flattened buttresses, on either side of a thickened disc on the frontal shield. (When brood chambers are developed between two distal zooids, the second lamina can be seen to be derived from a buttress supplied by each zooid.) Concurrently, the shields of both maternal and distal zooids are becoming thicker, and their areolar buttresses are fusing to form interzooidal funnels. As the first lamina extends distally, the second grows distally and proximally, contacting the distal part of the maternal zooid shield and fusing with it. At this stage it therefore appears that the second lamina is derived from the maternal zooid (see Pl. 2A). The cuticle covering the laminae expands, so that they both grow outward into a 'bubble' of cuticle-covered, interzooidal hypostegal coelome. At this point, the cuticle covering the basal side of the first lamina, and that covering the frontal side of the second lamina may become isolated, and appear as a trace in longitudinal thin-sections. Both laminae extend laterally and distally and begin to curve frontally. They are closely apposed, but a minute space is visible between them (see Pl. 2F). Concurrent thickening of the distal zooid gives the developing brood chamber the appearance of being sunken in its frontal shield. There is still apparently some coelomic contact underneath the cuticle on the frontal side of the first lamina, as further thickening sometimes occurs on the surface at this stage (see Pl. 2E, F). The combined areolar funnels of the two zooids continue to lengthen as the frontal shields thicken, and these extend as tubes beneath the two laminae. The tubes open into the hypostegal coelome surrounding the brood chamber distally and laterally (see Pl. 2F).

At this stage the two laminae fuse, so that the minute coelomic space between them is 'pinched out'. In sections of complete brood chambers it appears to have become filled with calcification. The fused laminae continue to grow frontally and then curve medially, forming the raised, globular brood chamber. Secondary calcification also proceeds rapidly on the 'outer' side of the brood chamber. The change in microstructure is abrupt and can be seen in sections to be of the same form as that developed on the frontal shield of the zooids. As general, now extrazooidal, thickening proceeds, the brood chambers become increasingly immersed but the funnels may remain visible (see Pls 1C, 6D). The brood chamber thus appears to be a type of highly modified, interzooidal, frontal bud, derived from at least two zooids. It differs from the type of brood chamber found in *Bugula neritina*, which is a kenozooid derived from the zooid distal to the maternal zooid (see Woollacott & Zimmer, 1972), and from the type described in *Crassimarginatella* by Harmelin (1973 : 472), where the inner layer is part of the distal wall of the maternal zooid, and the outer layer is developed from the frontal wall of the distal zooid.

Some variation in sequences of development and their relative growth rates has been seen. In *T. celleporoides* the earliest stages appear at the growing edge, often at the earliest calcification of the frontal shield of the distal zooid. In *T. oranensis* and *T. mucronata* one to three zooids, and in *T. robusta* and *T. spathulata* two to four developing zooids, may intervene between the growing edge and the earliest recognizable sign of brood chamber growth. Variation in rates of growth

Table 1 Characters used in analysis.

	Quantitative characters, as measured or counted				
1	Length of zooid				
2	Width of zooid				
3	Length of orifice				
4	Width of orifice				
5	Length of brood chamber				
6	Width of brood chamber				
7	Length of orifice of brooding zooid				
8	Width of orifice of brooding zooid				
9	Length of rostrum of interzooidal avicularium				
10	Length of rostrum of vicarious avicularium				
11	Number of oral spines				
12	Minimum number of foramina				
13	Maximum number of foramina				
	Qualitative characters	**0**	**1**	**2**	**3**
14	Form of colony		encrusting	unilaminar	bilaminar
15	Occlusion of frontal foramina		not occluded	occluded late in ontogeny	occluded early in ontogeny
16	Type of frontal thickening		general	funnels or blocks	
17	Suboral region	not thickened	thickened	mucro present	
18	Orifice	no condyles or lateral indentations	indentations and/or condyles	large condyles, proximal sinus	
19	Types of avicularia	all absent	interzooidal only	interzooidal and vicarious	
20	Similarity of mandibles of two types	absent or only one type	similar	dissimilar	
21	Orientation of interzooidal avicularia	absent	random to lateral	distinctly distal	
22	Shape of interzooidal avicularian rostra	absent	expanded distally	rounded distally	acute distally

of parts of the brood chamber are illustrated by differences between those seen in *T. celleporoides* and in *T. mucronata* and *T. robusta*. In *T. mucronata*, the first lamina appears earlier and grows more rapidly than the second lamina. In some cases, calcification of the second lamina does not seem to occur and it appears as a cuticular cover, which does not calcify until later in ontogeny, when the secondary calcification is deposited. In some colonies of *T. robusta* the second lamina grows more rapidly than the first, and may even appear before it. The relative rates at which brood chambers develop may be roughly estimated among colonies by counting the number of zooid generations intervening between the earliest and the most complete stages in the development of the two laminae. In *T. perplexa*, *T. spathulata* and *T. oranensis* this may be as few as one to two generations; in *T. celleporoides*, *T. mucronata* and *T. robusta* development is less rapid and three to four generations may be present. Secondary calcification is also more advanced at an earlier stage in *T. spathulata*, *T. brancoensis* and *T. oranensis* than in the other species. The earliest astogenetic appearance of brood chambers may be correlated with the overall size of the colony. Species which have rather small, discrete colonies tend to produce brood chambers early; for example, they are present by the sixth zooid generation from the ancestrula in *T. perplexa* and *T. spathulata*. Other species with very large, erect colonies produce their brood chambers later in astogeny. Young colonies of *T. robusta* and *T. oranensis* comprising ten generations of zooids had no brood chambers.

Canu & Bassler (1923 : 168) stated that the 'ovicell' was 'endozooecial'. In a later paper (1928a : 43) it was described as 'hyperstomial and closed by the operculum', a description followed by several authors, e.g. Osburn (1950 : 98). However, the 'ovicell' of *T. sparsiporosa* (Canu & Bassler, 1928a : 50) was described as 'not closed by the operculum'. The relevance of the terms 'endozooecial' and 'hyperstomial' in the light of recent work on the ontogeny and structure of brood chambers is discussed briefly below (p. 124). The closure of the brood chamber by the operculum is one of the characters which may vary within a single colony in some Bryozoa; its state is also dependent upon the growth form of the colony and its preservation. In all specimens examined here the operculum, when present, is at a distinctly lower level than the opening of the brood chamber when in a closed position. When half open, it nearly closes the brood chamber opening, but the position in life during brooding is not known from direct observation. Later in ontogeny, brood chambers become immersed by calcification and this may give an impression that they are closed by the operculum. In the *T. spathulata*-group of species the space between the closed operculum and the roof of the brood chamber is proportionally less than it is in other species. In *T. musaica*, for example, some brood chambers appear to be closed by the operculum, others do not, but this seems to be a variation caused by difference in position at death and on preservation.

Coding of characters and results of polythetic clustering

In order to evaluate the degree of similarity among character correlations thirteen quantitative characters were measured or counted, and states of nine qualitative characters coded, for forty samples, see Tables 1 and 2.

Characters in *Tremogasterina* likely to be observable in many Recent and all fossil specimens are restricted to those preserved in the calcified skeleton. In living or well-preserved Recent material, many more characters are present which could be used for comparison among samples. Study of ultrastructure may also provide more characters than those at present recognized. Parts of colonies where zones of astogenetic repetition are present are comparable; zooids of overgrowth layers, which may be the only material available, sometimes show no more microenvironmental variation than those of primary layers, and are here regarded as comparable. Zooids of erect parts of colonies tend to vary less in overall dimensions than those of encrusting parts, which may be microenvironmentally affected. The ontogenetic state of zooids is more directly comparable, but the degree of ontogenetic thickening of the frontal shield may differ in its expression among species and sometimes among specimens of populations of species which have developed under different environmental conditions.

Table 2 List of forty samples analysed (see also Appendix, p. 140).

No.	Name	Reference	No.	Name	Reference
1	*T. problematica*	A. H. Cheetham	21	*T. robusta*	1975.10.4.1
2	*T. maçonnica*	A. H. Cheetham	22	*T. robusta*	1966.9.2.2
3	*T. areolata*	NMV	23	*T. oranensis*	1973.3.22.33
4	*T. pouyetae*	UCB	24	*T. oranensis*	1964.9.1.34A
5	'*T. miocenica*'	A. H. Cheetham	25	*T. oranensis*	1927.10.30.11
6	*T. lanceolata*	USNM	26	*T. brancoensis*	1964.9.1.43
7	*T. lanceolata*	1911.10.1.1713 1932.3.7.61	27	*T. brancoensis*	1973.3.22.35
8	*T. mucronata*	1911.10.1.1692	28	*T. brancoensis*	1964.9.1.38
9	*T. mucronata*	1965.8.2.1 1966.1.6.1	29	*T. celleporoides*	1961.10.30.11
10	*T. mucronata*	1911.10.1.1698	30	*T. celleporoides*	1944.1.8.272 1963.2.12.281
11	*T. mucronata*	1931.5.2.6	31	*T. celleporoides*	1962.2.20.7
12	*T. mucronata*	USNM 9766	32	*T. spathulata*	1961.10.30.9 1965.9.4.1
13	*T. mucronata*	USNM Fowey Light	33	*T. spathulata*	1971.3.16.1A
14	*T. mucronata*	USNM Alb. 2319	34	*T. spathulata*	1939.2.4.1
15	*T. subspatulata*	USNM Alb. 3005	35	*T. musaica*	1970.2.8.9pt
16	*T. subspatulata*	USC (*T. magnipora*)	36	*T. perplexa*	1973.3.22.27
17	*T. subspatulata*	USNM	37	*T. spathulata*	Midway Id
18	*T. subspatulata*	USC	38	*T. spathulata*	DG8 China Sea
19	*T. robusta*	1936.12.30.42	39	'*T. miocenica*'	Chipola Fm.
20	*T. robusta*	1965.2.4.11	40	*T. spathulata*	1975.9.24.4

Actual and relative rates of growth are unknown and there is thus no absolute time scale available for deciding which groups of zooids are strictly comparable. Generally, the measurements and other observations used here were taken from ten zooids from a zone of repetition which did not show any microenvironmental influences such as crowding, etc. In the case of some Recent specimens, and practically all fossil colonies, no such exact conditions could be applied. Preservation of both fossil and Recent material also alters characters and makes some observations difficult. The characters and character states used here are given in Table 1, and the details of specimens coded in Table 2. Data, nearest neighbour and coordinate tabulations are stored at the British Museum (Natural History).

The following notes describe some of the characters used:

CHARACTERS 1 AND 2. During ontogenetic thickening of calcified walls, the limiting vertical walls of zooids become completely obscured (see p. 107). The length and width of zooids has therefore been measured from the distalmost edge of the orifice of one zooid to that of the next in direct distal sequence. Where even the edges of orifices were obscured or worn, the mid-point of common funnels in the calcification between zooids has been used as a demarcation in measuring both length and width of zooids.

CHARACTERS 3, 4, 7, 8 AND 18. As the frontal shield thickens, the orifice appears to become larger in some specimens, and its shape becomes less regular. Wherevere possible, measurements have therefore been made at the earliest ontogenetic stage after completion of the orifice and condyles. The very nature and relatively late ontogenetic development of the umbonuloid secondary orifice make it more susceptible to microenvironmental influences than the primary calcified orifice of its cryptocystidean counterpart. There may be a great deal of variation within a colony in orifice size and shape (see Pl. 5C), and in some species there is a slight but significant difference in the means and range of the orifice dimensions in brooding zooids. Condyle and 'sinus' development can be seen in all but very worn specimens.

CHARACTERS 5 AND 6. Brood chambers are frequently influenced by development of surrounding zooids. In addition, secondary thickening may radically alter measurements.

CHARACTERS 12, 13, 15 AND 16. The number of foramina is greatly influenced by ontogeny, but does seem to have some 'specific' correlations in range, if not in absolute number. Foramina may be subdivided or obscured during ontogeny, or surrounded singly or in groups by funnels and blocks of calcification; they are also susceptible to wear. The extent and type of frontal shield thickening does seem, within fairly wide limits, to be genetically controlled.

CHARACTERS 9, 10, 19, 20, 21 AND 22. Avicularian rostra are often much affected by wear in fossil specimens. Their orientation and rough dimensions are usually observable, and although the distal part of the rostrum is somewhat vulnerable, it is often well-preserved enough for its shape to be inferred in one or two examples in a colony. Variation in mandible shape among colonies of a species or population is common, variation within a colony occurs more rarely.

The results of clustering have shown that overall morphological similarity broadly parallels the groupings, and also indicates the apparent evolutionary trends, which were concluded from inspection. 'Anomalies' in cluster formation are interesting because they indicate the relative importance of some 'characters'. They also reveal possible inadequacies in the input of original data, and they illustrate the very close morphological similarity among some populations widely separated in space and time.

Of the ten clusters of samples which separated in three dimensions (see Fig. 5), only two, *T. lanceolata* (6 and 7) and *T. celleporoides* (29–31), were completely inclusive of samples nominally assigned to the species, and exclusive of any other sample. The cluster of *T. oranensis* samples (23–25) included one of *T. brancoensis* (27), which is not surprising, in view of the close morphological similarity of some, but not all, populations of these two species (see p. 134). The samples of

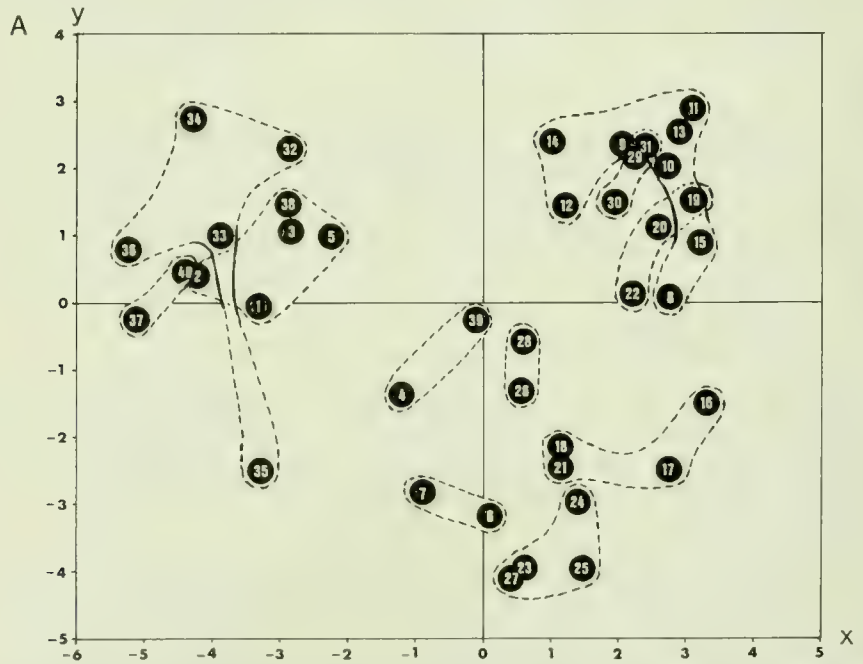

Fig. 5A Ordination diagram, prepared by the principal coordinate algorithm (see Gower, 1966). Squared distance in proportion to (100 – similarity). See Table 2 for key to numbering; data and coordinates stored at BMNH. Coordinates X, Y. Note separation of three clusters of 'fossil' and *T. spathulata* samples (1–3, 5, 32–38, 40) from remaining clusters.

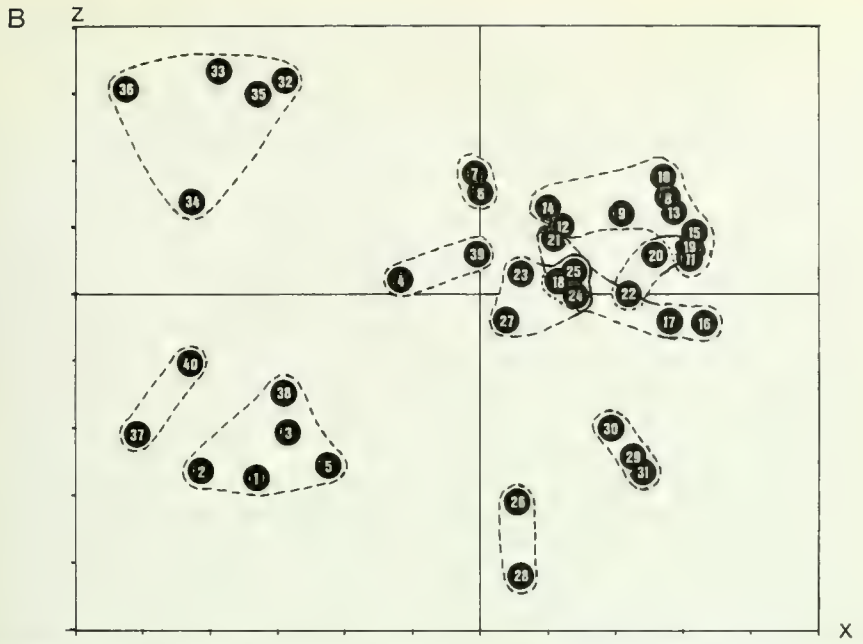

Fig. 5B Ordination diagram, as Fig. 5A. Coordinates X, Z. Note consistency of separation as in Fig. 5A, and in close association of *T. robusta* (19, 20, 22) and *T. mucronata* (8–14) clusters.

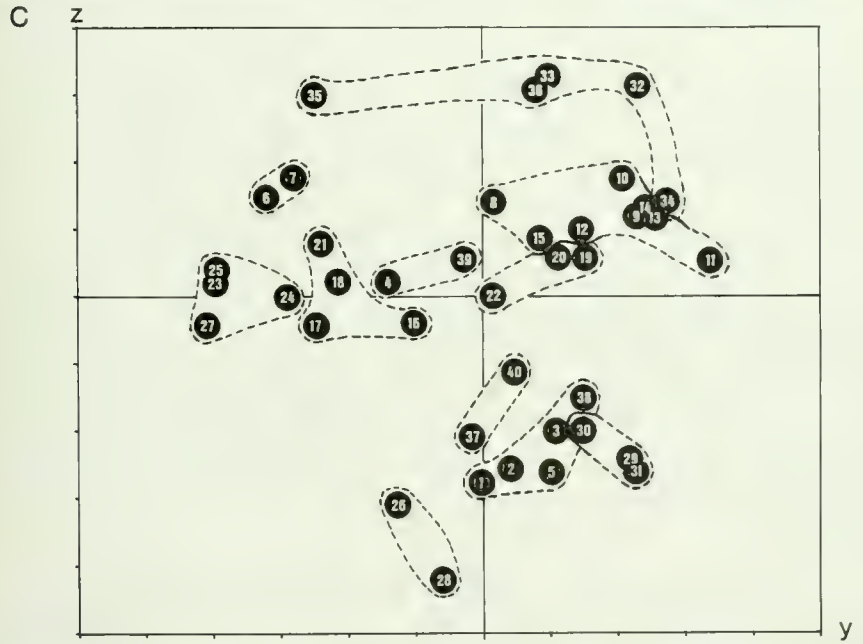

Fig. 5C Ordination diagram, as Fig. 5A. Coordinates Y, Z. Note consistent separation of small clusters (4, 39), (6, 7), (16–18, 21), (23–25, 27), (26–28) and (29–31).

T. mucronata from the Gulf of Mexico (8–14) clustered closely together, but included one sample of *T. subspatulata* (15). This cluster was well separated from that of the remaining Californian samples of *T. subspatulata* (16–18) which, however, included the ? Pleistocene sample of *T. robusta* from the Red Sea (21). The characters of these last two species are very similar, particularly in the size, shape and orientation of the avicularia and occlusion of frontal foramina. The deciding factor in the 'anomalous' position of the Red Sea sample appear to have been connected with zooidal size characters. The zooids of the ? Pleistocene sample are significantly smaller than those of other, Recent *T. robusta* specimens (see p. 134). These *T. robusta* samples (19, 20, 22) showed a very close association with the *T. mucronata*-cluster in three dimensions. Nearly all the 'fossil' samples (1, 2, 3, 5) clustered together, and included one sample of *T. spathulata* (38). Three of the remaining *T. spathulata* samples (32–34) formed a diffuse but distinct cluster with *T. perplexa* (36) and *T. musaica* (35). Exceptions to these two groups were *T. pouyetae* (4) and one sample of '*T. miocenica*' (39), and two samples of *T. spathulata* (37, 40) which formed two distinct clusters. Generally, these closely involved clusters of fossil and *T. spathulata* samples were well separated from all other samples as a sub-group. Here again, zooidal size characters appear to have been a deciding factor. The close morphological similarity between, for example, the sample of Recent *T. spathulata* (40) from the Seychelles and the Eocene *T. maçonnica* is, however, noted on p. 137 (see also Pl. 5A and Fig. 8A).

In order to test possible weighting by a preponderance of 'avicularian' and 'foramen' characters, and to test the relationships within the two major subgroups of clusters, three characters (Nos 13, 19, 20) were discarded and the *T. mucronata-subspatulata-lanceolata* samples were isolated and re-clustered, as were the 'fossil' and *T. spathulata* samples. In both cases, relationships within and among groups remained virtually unchanged.

The clusters illustrated in the ordination diagrams (Figs 5A, B, C) were constructed from the values for nearest neighbour pairs. Generally, percentage similarities among the samples was not very high. Among the highest was a value of 96% between *T. celleporoides* (29 and 31), 95% between *T. lanceolata* (6 and 7) and 93% between *T. subspatulata* (16 and 17), *T. mucronata* (9 and 10) and *T. oranensis* (23 and 25). Examination of the values for second nearest neighbour pairs emphasized the close similarity between other pairs of samples. For example, the 'anomalous' sample of *T. subspatulata* (15) had an 86% similarity with *T. mucronata* (13) but a very close, secondary similarity of 85% with *T. subspatulata* (16). The *T. oranensis* sample from Angola (23) had a 93% similarity with the sample from Cap Blanc (25) but an 89% secondary similarity with the Angolan sample of *T. brancoensis* (27). Similarly, although the 'anomalous' samples of *T. spathulata* (37, 40) had an 88% similarity with one another, the second nearest neighbour in both cases was the fossil *T. problematica*, at 84%, parallel with the 86% similarity between *T. problematica* and the *T. spathulata* sample from the South China Sea (38).

As mentioned above (p. 116), the number and nature of the characters available in comparison of fossil with Recent specimens is restricted, but it has become evident that all the characters used at present to distinguish species within *Tremogasterina* populations rely heavily upon isolation in time and space. Relationships among both the fossil and Recent representatives of the *T. mucronata*-complex, and among the *T. spathulata* samples, are examples of the difficulties inherent in assessing a fairly large number of individual samples, none of which is really complete enough to establish limits of intra-sample astogenetic and ontogenetic variation. Both intra- and interspecific variation and morphological similarities are pronounced within *Tremogasterina*; the samples are, however, separable in time and space. Although some of the criteria used here to divide populations are arbitrary and possibly not consistently applied, the groupings attained both by clustering and by inspection have been used here as the basis of the tentative evolutionary series given below.

Evolutionary trends and distribution in time and space

In the absence of large and widely distributed populations of fossil specimens, any attempt to reconstruct the evolutionary history of the genus can be only of the most tentative kind. There are indications, however, that two major, divergent trends in morphological change may have occurred.

The first was towards increase in the number of frontal foramina, while retaining the characters of encrusting habit and small zooid and avicularium size typical of the earliest known fossil specimens. This resulted in the Recent forms like *T. spathulata*, *T. perplexa* and *T. musaica*. The second trend was towards a reduction in the number and extent of frontal foramina, ending in their occlusion early in ontogeny. This was accompanied by considerable development of extra-zooidal tissue, allowing the potential for an erect habit, and was accompanied in some forms by an increase in the size of the zooids and the avicularia, which last became more regularly distal in orientation. This resulted in the Recent forms like *T. mucronata*, *T. lanceolata*, *T. robusta* and *T. oranensis*.

The Eocene species, *T. maçonnica*, is of great interest in that it combines some of the characters of both these trends. The small zooids are encrusting, and the foramina have distinct rims of calcification in some cases, similar to the early stages of the formation of blocks of calcification seen in the *T. spathulata*-group. At the same time, the number of foramina is far lower, and the orifice has the rounded, non-sinuate shape found in later populations of *T. mucronata*. The orifice in *T. maçonnica* also resembles that of some cribrimorphs and *Arachnopusia* in appearance. There is a distinct, raised, proximal apertural bar, and the distal part of the orifice slopes in a basal direction away from this level. Similar orificial characters are present in the primary distal zooids budded from the ancestrulae of several Recent species (see Fig. 1), which suggests that this may be a 'primitive' character state. Elongation of the orifice, and the appearance of a proximal 'sinus', occurs in the Miocene *T. pouyetae*, but reaches its greatest development in both the *T. spathulata* group (in *T. musaica*), and in the *T. mucronata–lanceolata–robusta* group (in *T. oranensis*).

Umbonuloid species do not seem to form multilaminar or erect colonies by colony-wide frontal budding, as do many cryptocystidean forms. Frontal budding occurs sporadically, and is followed by overgrowth layers. Cheetham (1971) has analysed the correlation of methods of thickening and strengthening the frontal wall in cheilostomes with the evolution of the erect habit. Most Recent species of *Tremogasterina* have encrusting, multilaminar colonies, which rise into unilaminar, often tubular, erect expansions. These are often thickened by overgrowth layers. The same form of growth occurs in *T. oranensis*, but *T. brancoensis* is truly bilaminar, although here too, the erect branches are later strengthened areas by of overgrowth.

It is inferred here that the descendants of the earliest Atlantic populations (*T. problematica*, *T. maçonnica*) gave rise to the Miocene populations represented on the one hand by '*T. miocenica*' and *T. mucronata* in North America and the Gulf-Floridan region, and on the other hand by *T. areolata* and *T. pouyetae* in southern Europe. The wide Recent distribution and intraspecific diversity of populations of *T. spathulata*, coupled with the one Pliocene record from Midway Is., suggest that it, too, may have been derived from an extensively distributed, *T. maçonnica*-like form. The possibility that the Recent west African *T. perplexa* and *T. musaica* are similarly derived is purely speculative. The similarities in zooidal and orificial characters among the Miocene *T. areolata* and *T. pouyetae* and the ? Pleistocene-to-Recent *T. robusta* populations indicate that they may be related. If so, this *T. robusta* group is a further example of the migration (or more probably of the progressive restriction) of shallow-water, southern European Miocene forms to the Indo-Pacific region (see Lagaaij & Cook, 1973). *T. robusta* also has features in common with the *T. oranensis–T. brancoensis*-complex, but the absence of African fossil specimens precludes any inferences as to the closeness of this relationship. Without fossil evidence it is also impossible to suggest a derivation for the Recent western Pacific populations of *T. celleporoides*. There is apparently no Tertiary record of *Tremogasterina* from Australia (see p. 123), and generally, the characters of *T. celleporoides* have more in common with those of *T. mucronata* than with those of *T. robusta*, although it seems unlikely that it could have been derived from the American species complex.

Geographically, the Recent forms fall into three distributional groups (see Maps 1, 2, pp. 145, 146). In the Indo-Pacific (*T. spathulata*, *T. robusta*, *T. celleporoides*), *T. spathulata* has the most extensive, and *T. celleporoides* the most restricted range. In the eastern Atlantic (*T. oranensis*, *T. brancoensis*, *T. perplexa* and *T. musaica*), the first two species have a wide range and form an interesting complex which may show either divergence or convergence of characters (see p. 135).

T. perplexa and *T. musaica* are as yet known from few records, but probably have a larger range in this area. The third group of populations extends through a large area from Florida and the Gulf of Mexico, the Caribbean and Brazil, to California, western Mexico and Panama. The populations are here grouped together as three species-groups (*T. lanceolata*, *T. mucronata*-complex and *T. subspatulata*). It is interesting that whereas very similar species included in the *T. spathulata*-group are present in the eastern Atlantic and Indo-Pacific, there is apparently no Recent record of any similar form from the western Atlantic or eastern Pacific region. An Oligocene form, *Arachnopusia vicksburgica*, was however described from the Vicksburgian of Mississippi by Canu & Bassler (1920 : 311, pl. 85, figs. 1–3) The colonies were rare; they encrusted shells, and had large zooids (Lz 0·65–0·72 mm), with ten to fifteen frontal foramina, each surrounded by a polygonal area of calcification. No oral spines were mentioned, and the 'hyperstomial' brood chambers were covered by calcification which in the retouched figures resembles the blocks of secondary tissue found in *T. musaica*. Small, rounded, interzooidal avicularia were present. It is possible that *A. vicksburgica* is related to the *T. spathulata*-group of species, but it requires further investigation.

Many of the species, both fossil and Recent, are associated with oyster shells, although coral is also a frequent substratum. *Tremogasterina* typically extends into shallow water, but the distribution of several species descends into deep water, and *T. robusta* is the only form confined to depths of less than 37 metres (see Powell, 1967 : 166). The known depth ranges are given in Table 3.

Table 3 Depth ranges of *Tremogasterina* spp.

Species	Depth range in metres	Species	Depth range in metres
T. robusta	0–37	*T. subspatulata*	9–104
T. musaica	50	*T. lanceolata*	146–271
T. perplexa	50	*T. celleporoides*	0–420
T. brancoensis	50–73	*T. spathulata*	0–430
T. oranensis	20–100	*T. mucronata*	60–506

Relationships among umbonuloid cheilostomes

The sequence of changes in the ontogeny of the frontal shield in *Tremogasterina* resembles both that in *Triporula* and *Exechonella* (see Cook, 1967) and that in *Adeona* (see Cook, 1973). These three genera differ from *Tremogasterina* in the absence of oral spines and external brood chambers.

Some of the species here assigned to *Tremogasterina* have been previously placed in *Hiantopora* and *Arachnopusia*. The characters and limits of these two genera need investigation and revision. Generally, *Hiantopora* differs from *Tremogasterina* in that the frontal shield develops asymmetrically and unilaterally. It is composed of anastomosing spinous processes which are calcified both frontally and basally, with an intervening coelomic space. Development in *Arachnopusia* is very similar to that in *Tremogasterina*. The calcified frontal shield is umbonuloid and consists of branching and anastomosing processes. The frontal septulae are minute but do not extend distally round the secondary calcified orifice. The sequence of developmental episodes in the oral region differs from those in *Tremogasterina*. Zooids at the growing edge show that the oral spines, which often develop unilaterally, are differentiated before the delineation of the secondary calcified orifice is complete. The brood chambers, too, are well developed at this stage. In *Tremogasterina* brood chambers may develop early in ontogeny, but not before the partial completion, at least, of the frontal calcified shield of the next distal zooid.

Hiantopora liversidgei Tenison Woods (1876 : 149) resembles *Tremogasterina* in possessing one to three large, reniform frontal foramina. Specimens in the British Museum (Balcombe Bay, Victoria, Miocene D35451) show what appears to be a unilateral spine base preserved in some zooids. The brood chambers and adventitious avicularia are very similar to those found in species

assigned to *Arachnopusia*, and this is almost certainly where its affinities lie (see Brown, 1952 : 178). Waters (1881 : 328) described *A. liversidgei* as '*Mucronella mucronata* Smitt', this suggesting that it was identical with the Recent Floridan species belonging to *Tremogasterina*. At present, no Tertiary form of *Tremogasterina* is known from the Australasian region.

As noted below (pp. 135, 136), two of the species here included in *Tremogasterina* were originally assigned to *Lepralia*, and later considered to belong to the cryptocystidean ascophoran genus, *Cleidochasma* Harmer (see Cook, 1964 : 11). There is increasing evidence of parallel series of genera, with species which have many similar characters, but which seem to have evolved convergently. These genera have alternatively either umbonuloid or cryptocystidean frontal shield ontogeny. This distinction is not a monothetic one, but involves many character correlations of body wall layers, ontogenetic sequences and orificial relationships.

In addition to the *Adeona–Adeonella* and *Tremogasterina–Cleidochasma* series, recent investigations have shown that among the overwhelmingly cryptocystidean 'smittinid' genera, there are also forms which have umbonuloid development. The 'smittinid' genera include a wide diversity of forms (see Osburn, 1952; Ryland, 1963; Soule & Soule, 1973), but have a single character in common. This is the presence of a well-developed proximal oral denticle (lyrula). The species described by Powell (1968 : 2303, pl. 9, fig. d) as *Escharella thompsoni* Kluge is represented in the British Museum collections by specimens from southern Greenland (Nanortilik, 110 metres, 1969.3.24.19–22), which have well-preserved growing edges showing complete ontogenetic series of umbonuloid development. The type-species of *Escharella*, *E. immersa* (see Ryland, 1963 : 18), is cryptocystidean. Similarly, the species described by Calvet (1909 : 32, pl. 3, fig. 7) as ? *Phylactella lyrulata* is represented in the British Museum Collections by specimens from the Antarctic (McMurdo Sound, 45–366 metres, 1967.2.8.136, 138 and eastern edge of ice barrier, 162°30″ W, 182 metres, 1967.2.8.137) which, unlike the type-species of *Phylactella*, *P. labrosa* (see Ryland, 1963 : 18), have umbonuloid frontal shield development. In both these forms the basal part of the umbonuloid fold advances as a continuous sheet of calcified tissue. The completed frontal shield has no foramina, but there is peripheral series of areolae derived from frontal septulae alternating with raised buttresses, very similar to that illustrated by Cheetham (1968, pl. 10, fig. 3) in the umbonuloid genus *Metrarabdotos*. This form of shield is also found in specimens of *Coleopora seriata* Canu & Bassler (1929, BMNH, 1931.12.38.87) and in the specimens from Borneo (BMNH, 1851.1.20.11), described as *Teuchopora* sp. by Harmer (1957 : 898, text-fig. 97). Other specimens of *Coleopora*, such as those described by Harmer (1957 : 898) as *Teuchopora verrucosa* (Canu & Bassler, 1929), which are part of Canu & Bassler's material of *C. verrucosa* from the Philippines (BMNH, 1931.12.30.85), have an umbonuloid frontal shield development with foramina similar to that of *Exechonella*. Thus, even within one nominal generic grouping of umbonuloid species there are differences in frontal shield ontogeny which may indicate that in spite of general similarities in colony form and zooid appearance, there may be little systematic relationship among the specimens.

Problems arising and further fields of work

Apart from the nomenclatural problems inherent in the descriptions of the type and other species (see p. 125), study of *Tremogasterina* has revealed several aspects of morphology and distribution which require further work.

One of the principal problems in current cheilostome systematics is the establishment of correlations between structures associated with the ontogeny of the calcified frontal shield and the hydrostatic apparatus, which would be recognizable in fossil specimens. Some preliminary correlations which allow tentative inferences have been noted by Cheetham (1968), Banta (1971) and Cook (1973). The umbonuloid ontogeny and basically anasciform affinities of some of the species now assigned to *Tremogasterina* were not recognized until complete ontogenetic series were available. It is possible to infer umbonuloid ontogeny from isolated episodes and from a correlation of characters such as frontal septulae and the form of the secondary calcified orifice (see also Cook, 1973). The nature of the ontogenetic sequences and the homology of the layers involved are not always observable in fossil or Recent material in an advanced state of calcifica-

tion. At present, there are few criteria available allowing inferences on ontogeny to be made from such specimens. The confluent nature of the hypostegal coelomes perhaps allows only the generalization that at any point above frontal septula, some form of interzooidal frontally budded structure is possible. The presence of a hypostegal coelome itself may be inferred in specimens without 'soft parts' from the coalescence of areolae and eventual colony-wide extrazooidal calcification. It is probable that specimens of fossil forms exist in which the frontal foramina are occluded, and the orifice is elongated, with large condyles and a proximal sinus, like *T. oranensis*. Conversely, species like *T. spathulata*, with a large number of foramina surrounded by blocks of calcification, may be found as fossils in the future. Their recognition as forms belonging to *Tremogasterina* may depend entirely upon the presence of a series of zooids showing the frontal shield ontogeny. Large gaps are also present in the known geographical distribution and fossil record. A range of Eocene to Pliocene specimens from western Africa, southern Europe and the Indian Ocean at least would be necessary to trace the history of the many Recent forms. Now that some of their characters have been recognized, it is possible that the affinities of some of these forms may be traced in the future. Further examination of both Recent and fossil oyster and coral faunas for encrusting Bryozoa would be one of the first steps in the search for specimens showing morphological states linking known forms in time and space.

Work on microstructure and ultrastructure of the calcified walls may yield characters and character states which can be correlated with known ontogenetic sequences. Preparation of thin-sections of hard and soft parts of known relationship *in situ* is the first step in discovering such correlations.

The tracing of the ontogeny of the brood chambers from Recent, well-preserved material raises the problem of terminology of such structures in less complete fossil and Recent material. The terms 'hyperstomial' and 'endozooecial', for example, derive from the concept that the brood chamber is necessarily 'part of' the proximal zooid, i.e. the zooid which produces the ovum which is to be brooded. Recent work by Woollacott & Zimmer (1972) has confirmed that some brood chambers are in fact kenozooids derived from the zooid *distal* to that which produces the ovum, and in communication with the distal zooid through septulae. Harmelin (1973) has also shown that an apparently 'hyperstomial ovicell' may be constructed of elements derived from both the maternal zooid and from the distal zooid, and that the brood chamber cavity is basically 'within' the distal zooid and thus 'endozooecial'. It seems that until many more ontogenetic series have been described, general terms which infer zooid relationships should be used with caution, and when used should carry with them the connotation that developmental series were not available for observation in the material described.

Other problems in recognition of structures of differing ontogeny, but similar appearance at full development, are involved in the description of communication pores. As noted above (p. 110), it would appear that pores with chambers may be part of a continuum of structures, and the terms 'diatella' or 'pore chamber' should also be used with caution.

However convenient all such terms may be in describing a structure, they do tend to obscure investigation of the actual developmental relationships concerned.

A study of variation both within and among populations should be made, using more plentiful material with more ecological data than that so far available. More characters would arise for comparisons, and in conjunction with studies of fossil specimens might lead to a reconstruction of the systematic relationships and evolutionary trends which would approach more closely to the real relationships and ecology of the group than that inferred here.

Systematic section

The genera *Poricella* and *Tremogasterina*

Both genera were originally erected by Canu; *Poricella* for *P. maçonnica* (Canu, 1904 : 28, pl. 35, fig. 43, from the Eocene of southern Tunisia), and *Tremogasterina* for *T. problematica* (Canu, 1911 : 256, pl. 7, figs 12, 13, from the Paleocene of Argentina, see p. 127).

These two species are considered here to be congeneric, and therefore it would appear that *Tremogasterina* is a junior subjective synonym of *Poricella*. However, the descriptions and characters of the type-species of both genera pose several problems of interpretation and nomenclature, and complete elucidation requires detailed examination of the type-specimens, and of other specimens involved. It is therefore not proposed here to introduce any formal designations, but to summarize briefly the history of the two genera and to indicate the problems arising.

Poricella was defined by Canu (1904 : 28) in the following terms: 'Zoécies convexes, perforées de plusieurs micropores. Apertura semi-lunaires. Génésies de même forme que les autres zoécies, mais de dimensions plus grandes et perforées par un plus grand nombre de pores. Avicellaires intercalés. Lutétien, Actuelle. Affinités. Ce genre comprend les trois sortes de zoécies qui caractérisent la famille des Adéonées de Busk. Ses perforation dorsales le rapprochent des Hiantoporidées de MacGillivray, mais elles n'ont peut-être pas la même fonction.'

The designated type-species, *P. maçonnica*, an Eocene fossil, was the only species assigned to the genus. No Recent ('actuelle') species or specimens were described, and as *P. maçonnica* was encrusting, no basal ('dorsale') perforations were mentioned. The description of *P. maçonnica* included the remarks: 'Perforations frontales au nombre de trois, en triangle sur les zoécies ordinaires et plus nombreuses sur les génésies. Génésies de dimensions plus grandes. Avicellaires intercalés, plus petits que les zoécies, assez rares.'

The term 'génésies' was used consistently by Canu for enlarged, dimorphic zooids with internal ovisacs, as found in the Adeonidae. The term he used for external, calcified brood chambers was 'ovicelles'. The figure of *P. maçonnica* (Canu, 1904; pl. 35, fig. 43) has been retouched, but shows approximately twelve zooids clearly. Two zooids have broken, but distinct 'hyperstomial ovicells', and none of the zooids is obviously dimorphic in any way, nor do any of them have more than three frontal pores. Photographs of the type-specimens of *P. maçonnica*, kindly supplied by Dr A. H. Cheetham, show zooids and numerous brood chambers very like the 'ovicells' in Canu's figure (see Pl. 3C, D).

In the section on the affinities of *P. maçonnica* Canu remarked 'J'ai trouvé dans le bassin de Paris une espèce très voisine qui n'est pas encore décrite.' It is possible that part of his generic definition and even of his description of *P. maçonnica* was based on specimens of this species, which had 'génésies', but which was not in fact formally described until several years later. In a subsequent paper on fossil species from Paris, Canu[1] (1907 : 150 (sep. p. 46), pl. 6, figs 5–8, text-fig. 3) introduced *Poricella elongata* from the Ypresian and Lutetian, and included *Mucronella sutneri* Koschinsky in *Poricella* (Canu 1907 : 47, pl. 9, fig. 1, text-figs 4, 5). Canu's (1907) figures of *P. elongata* are of a typically 'adeonid' species, and one (fig. 8) specifically shows the 'génésies'; large dimorphic brooding zooids. Koschinsky (1885 : 57, pl. 3, fig. 9) had given an excellent figure of *M. sutneri*, showing that it too, is an 'adenoid' species.

The concept of *Poricella* as a genus possessing dimorphic brooding zooids, in spite of the characteristic 'ovicells' present in the type-species, was emphasized by Canu in 1907, in his discussion of the genus. He remarked 'J'ai crée ce genre en 1904 pour une espèce du Tertiare de Tunisie, mais en ajoutant que certaines espèces fossiles et actuelles pouvaient y être introduites. M. Waters me fit alors constater' (presumably in a personal communication) 'que ce genre faisait double emploi avec *Hiantopora* MacGillivray. Malgré des anologies évidents, je crois cependant devoir maintenir le genre *Poricella* qui diffère de l'autre par la présence de génésies, c'est-à-dire, de deux sortes de zoécies à fonctions distinctes comme dans toutes les Adéonées de Busk.' Waters (1912 : 497) appears to have eventually accepted this statement, as he remarked 'There are gonoecia' (i.e. 'génésies') 'in the fossil *Poricella* Canu.' Subsequent records of *Poricella*, for example that of *P. davidi* Balavoine (1960 : 248, pl. 7a, fig. 5), are also of 'adeonid' species.

The further history of *Poricella* has extended the confusion. Canu & Bassler (1920 : 558, fig. 166N), included copies of Canu's text-figure of 1907 of *P. elongata*, when illustrating the characters of another adeonid genus, *Bracebridgia*. They did not, however, include either *P. elongata* or *P. sutneri* in the list of species they attributed to the genus (p. 567). In the same paper (p. 564) they included *Poricella*, with other genera 'which may be admitted as artificial subgenera in order to

[1] For dating and pagination of the various parts of Canu (1907–1910), see Reference section.

facilitate classification' in *Adeonellopsis*, and listed *P. maçonnica* as belonging to that genus. Canu & Bassler (1928a : 44-45) included *P. maçonnica* in *Tremogasterina* (see below), but Bassler (1935 : 174 and 1953: G213) continued to regard *Poricella*, with its type-species *P. maçonnica*, as 'a synonym or subgenus of *Adeonellopsis*'.

Examination of type and other specimens may show that some or all adeonid species presently assigned to *Poricella* could be placed in *Adeona* or *Adeonellopsis*. If any of them are distinct, however, it will be necessary to erect a new genus to accommodate them.

Tremogasterina was defined by Canu (1911 : 256) in the following terms: 'Frontale perforée par une grande ouverture qui en occupe presque toute la surface.' *T. problematica* was described with a frontal foramen larger than the orifice, which was wider than long. Small elliptical or fusiform interzooidal avicularia were present, with paired condyles. The ovicell was subglobular, not prominent, and opened into the interior to the zooid. Unfortunately, the zooids figured by Canu (1911; pl. 7, figs 12, 13) are practically unrecognizable. The photographs show fairly regularly arranged zooids, with small, randomly orientated avicularia. The specimen was obviously very worn and little more of its characters can be seen. Some specimens of a species of *Tremogasterina* are now known from the type-locality of *T. problematica*, they are discussed below (p. 127).

The nature of the brood chambers in *Tremogasterina* continued to be obscure. Canu & Bassler (1923 : 168, pl. 24, figs 3, 4) described *T. horrida* from the Miocene of Florida with 'endozooecial ovicells', and stated that 'the ovicell is concealed' in their description of the genus. Their specimens did not have ovicells 'in a condition to be photographed', but in the same paper they described '*Cribrilina cuspidata*' from the Miocene of Cuba (p. 88, pl. 15, fig. 16) with 'hyperstomial ovicells' and noted that it was 'very little distinct from *Escharipora mucronata* Smitt'. They seem to have overlooked the very obvious similarities between the two Miocene species at this time, but in their later paper on the fauna of the Gulf of Mexico (1928a : 43-44), they gave *T. problematica* Canu, *P. maçonnica* Canu, *E. mucronata* Smitt and *L. areolata* Reuss, together with *T. horrida* and *C. cuspidata* in a list of species included in the genus *Tremogasterina*. All these forms are considered here to belong to *Tremogasterina*, but one species included by Canu & Bassler (1928a), '(*Galeopsis*) *convexus* Canu & Bassler 1920', does not appear to belong to the genus.

TREMOGASTERINA Canu, 1911

Type-species *T. problematica* Canu.

The character correlations defining *Tremogasterina* as used here are as follows. Colony encrusting and erect, with secondary overgrowths of zooids arising from frontal buds. Ancestrula membraniporiform. Zooids with umbonuloid development of the frontal shield, developing from a curved lamina which forms a secondary calcified orifice and large proximal foramen by anastomosis of paired lateral processes. Secondary calcified orifice large, with lateral indentations and frequently with lateral condyles. Oral spines present, oral shelf slight or absent. Frontal foramina often subdivided, remaining open or uncalcified in some forms, becoming occluded at various stages in the ontogeny of others. Secondary thickening of the frontal shield usual, sometimes resulting in the development of a suboral mucro and/or calcified ridges. Zooids communicating by distal and lateral multiporous septulae, which become surrounded by deep, calcified buttresses during ontogeny, sometimes forming chambers similar in appearance to diatellae. Zooids with a row of frontal, marginal multiporous septulae, which frequently extend distally completely round the orifice. Frontal septulae becoming obscured in late ontogeny, or surrounded by buttresses of calcification, eventually coalescing to form interzooidal funnels. Avicularia interzooidal, arising from frontal septulae of adjacent zooids; vicarious avicularia often also present. Mandibles hinged on a complete bar or on long, spinous, paired processes. Brood chambers arising as modified interzooidal frontal buds from the frontal septulae of sequential zooids, prominent at first ('hyperstomial'), becoming immersed by secondary calcification, not closed by the operculum.

Remarks. Species are included in which the frontal foramina are present only at the earliest ontogenetic stages, and become occluded during ontogeny. Although fossil colonies here attributed

to *Tremogasterina* are fairly plentiful, they have been recognized only as forms with open frontal foramina. Complete occlusion of the foramina results in such a different appearance that relationships can only be traced where ontogenetic series are available, as in the Recent species *T. oranensis* and *T. brancoensis*. Consequently, it is possible that fossil forms with occluded foramina occur, but have not yet been recognized as belonging to *Tremogasterina*.

Tremogasterina problematica Canu

Tremogasterina problematica Canu, 1911 : 256, pl. 7, figs 12, 13, Rocanéen de Roca, Argentina, Paleocene (see below).

Material examined. Photographs of *Tremogasterina* sp. from the type-locality of *T. problematica* (see below).

Description (Pl. 3A, B). This description is based on that of Canu (1911) together with observations based on photographs of a species of *Tremogasterina* kindly supplied by Dr A. H. Cheetham. Colony encrusting, frequently on oyster shell. Zooids with a flat frontal shield rising distally to a thickened bar proximal to the orifice. Orifice rounded distally, straight proximally, with no obvious mucro or condyles. Two distal oral spines present in brooding zooids. Frontal shield with one to five foramina. Funnels present between zooids, and chambered septulae present. Avicularia interzooidal, subrostral chambers not much raised, placed near zooid orifices and oval in shape, orientated randomly. No bar or condyles seen. Brood chambers not very prominent, imperforate frontally.

Measurements (in mm).

Lz 0·42–0·50	Lo 0·11–0·14	Lov 0·18–0·19	Lr 0·07–0·10
lz 0·20–0·30	lo 0·11–0·13	lov 0·18–0·21	

Remarks. Canu gave the age of the Roca formation as Cretaceous. Buge (1946) has discussed the age of some of the Argentinian formations from which specimens were described by Canu in 1908, but not those described in 1911. Bertels (1969) gave the age of the Roca formation as Paleocene (Lower Danian). Dr A. H. Cheetham (*pers. comm.*, 1975) has informed me that 'according to Dr Bertels (*pers. comm.*, 1969) the type-locality for the Bryozoa described by Canu is Barranca del Jaguël, Neuquén Province'. Dr Cheetham has examined a sample of material from this area, and has found the specimens of *Tremogasterina* sp. figured here on Pl. 3A, B. Canu's figures (1911 : pl. 7, figs 12, 13) are of a specimen so worn as to be practically unrecognizable, but if it does belong to *Tremogasterina* as defined here, it appears almost certain that the specimens examined by Dr Cheetham are of *T. problematica*.

Tremogasterina maçonnica (Canu)

Poricella maçonnica Canu, 1904 : 28, pl. 35, fig. 43, Tunisia, Eocene.
Tremogasterina maçonnica Canu, see Canu & Bassler, 1928a : 44.

Material examined. Photographs of the type-specimen of *T. maçonnica*.

Description (Pl. 3C, D). Colony encrusting oyster shell, with overgrowth layers. Zooids small, with rounded frontal shields. Orifice with lateral indentations and a small proximal mucro on a distinct, thickened suboral bar. Three to four frontal foramina, rounded or lunate, sometimes occluded, with distinct rims and suture lines. A few interzooidal funnels present, little general thickening. Avicularia numerous, small, with rounded rostra and a bar, orientated randomly. Brood chambers (all broken) 'hyperstomial'.

Measurements (in mm).

Lz 0·30–0·33	Lo 0·07–0·10	Lov 0·12–0·14	Lr 0·06–0·10
lz 0·20–0·22	lo 0·10–0·12	lov 0·13–0·15	

Remarks. I am indebted to Dr A. H. Cheetham, who provided the photographs of Canu's type specimen illustrated here on Pl. 3C, D. They show that the very small zooids have well-preserved orifices and frontal shields, particularly in those of the overgrowth layer. The large foramina

appear in many cases to be bordered by rims of calcification like those of *T. spathulata*, *T. perplexa* and *T. musaica*. The secondary calcified orifice slopes distally toward the basal wall, and there is a distinct, thickened suboral bar, as in many Cribrimorpha. Similar zooids are found in the ancestrular region of other species (see pp. 106, 121 and Fig. 1). Avicularia are small and randomly orientated; the bar is visible in many cases. All the brood chambers are broken frontally; they are raised, 'hyperstomial', and do not appear to have been closed by the operculum.

The exact locality of *T. maçonnica* was given as 'Lower Eocene, Djebel Blidji vers le Nord, sur *Ostrea punica*'. Although it seems very probable that other, more southerly African fossil specimens of *T. maçonnica* remain to be discovered, none were reported by Gorodiski & Balavoine (1961) from the Eocene of Senegal. No fossil specimens of *Tremogasterina* were found from the Upper Miocene of Loanda by Buge & Galopim de Carvalho (1964).

Fig. 6 European Miocene *Tremogasterina*. (A) *T. areolata* (Reuss). Drawn from the type-specimen, NMV, Baden, Austria. Zooids showing elongated orifice, brooding zooids with dimorphic orifices and avicularia incorporated into the calcification of the brood chamber (cf. Fig. 8B, '*T. miocenica*'). (B) *T. pouyetae* sp. nov. Drawn from the holotype specimen, UCB, Hérault, France. Zooids showing elongated orifices and numerous frontal foramina (cf. Pl. 4C). Scale = 0·50 mm.

Tremogasterina areolata (Reuss)

Lepralia areolata Reuss, 1874 : 156, pl. 4, figs 9, 10.
Tremogasterina areolata (Reuss), Canu & Bassler, 1928a : 44. David & Pouyet, 1974 : 112, pl. 6, fig. 7.

MATERIAL EXAMINED. Type. NMV, specimens on *Porites incrustans*, Baden, Austria, Miocene.

DESCRIPTION (Fig. 6A). Colony encrusting. Zooids small with rounded frontal shields. Orifices elongated, with four spine bases and a small proximal mucro present in some zooids. One to four frontal foramina present. Avicularian rostra raised, rounded, occasionally truncate or pointed, randomly orientated, with a bar. Vicarious avicularia present. Brood chambers prominent.

MEASUREMENTS (in mm).

Lz 0·33–0·48	Lo 0·15–0·16	Lov 0·12–0·15	Lr 0·08–0·15
lz 0·28–0·39	lo 0·12–0·13	lov 0·16–0·18	Lvic 0·30–0·45

REMARKS. The type-specimens consist of two colonies, one of approximately 2000, the other of approximately 400 zooids. Neither colony has an ancestrular region preserved and there are areas of overgrowths and also microenvironmental changes in shape, size and orientation of zooids, etc., due to crowding by other bryozoan species and irregularities of the substratum. Crowding is caused by colonies of ten other species present, but some uninterrupted growing edges have been preserved. These show that the zooids have one to two distal and two lateral large, chambered

septulae, and twenty-five to thirty frontal septulae which extend round the distal end of the zooids. The frontal calcified shields are inflated, and finely granular; the central areas are slightly depressed, and have one to four foramina. Foramina are most frequently double, or single and trifoliate. Ontogenetic thickening of the frontal shield is not very extensive, and the common funnels between zooids are not separated by prominent bars of calcification. The orifices are distinctly elongated, and in many zooids the paired condyles are expansions from a ridge which is continuous distally below the level of the outer calcification (see Fig. 6A). There are four oral spine-bases and a small proximal mucro is often present. Avicularia occur somewhat irregularly among zooids and are small but very prominent. The subrostral chambers are considerably raised above, and the rostra are parallel to, the level of the zooidal frontals. The distal part of the rostra are usually rounded, but some are broadly truncate and others apparently pointed. The orientation of interzooidal avicularia is very variable, but there is a tendency to be distally or laterally directed. A few examples have a complete bar; in others this may have been broken and worn, and the avicularia appear to have small condyles. Vicarious avicularia are present, but very rare, occurring in the proportion 1 : 500 zooids; they have wide rostra and no bar. Brood chambers are frequent, often occurring in groups; approximately 100 are present. Orifices of brooding zooids are slightly dimorphic, being wider than those of autozooids. The brood chambers are small, finely tubercular and very prominent. A laterally placed avicularium is characteristically incorporated by ontogenetic thickening into the calcification of the brood chamber (see Fig. 6A).

Tremogasterina pouyetae sp. nov.[1]

Material examined. Holotype. UCB Bz52 Tourbes: Saint Jean (Hérault), S.W. France, Helvetian, Miocene. Paratypes Bz61 Nezignan l'Eveque (Hérault), Molasse, Marns Sableuse, and Bz42, 43, 44, all Helvetian, Miocene.

Description (Pl. 4C, Fig. 6B). Colony encrusting oyster shell. Zooids large, with inflated frontal shields. Orifice elongated, with condyles and four to six oral spines, but no mucro. Three to eight small frontal foramina. Avicularia raised, with truncate or rounded rostra, usually orientated distally; vicarious avicularia not seen. Brood chambers small, prominent.

Measurements (in mm).

Lz 0·42–0·68	Lo 0·16–0·18	Lov 0·20	Lr 0·18–0·24
lz 0·30–0·36	lo 0·12–0·14	lov 0·22	

Remarks. The colonies encrust both the inner and outer sides of oyster shells. There is a total of approximately 5000 zooids present. No ancestrulae are present and areas of overgrowth are common, but the growing edges of the primary lamina are not crowded, although colonies of *Onychocella angulosa* and other species are present. Zooids at the growing edge show that there are one to two distal and two to three lateral chambered septulae, and fifteen to twenty-six frontal septulae. These extend distally round the zooidal orifice. The frontal calcified shield is inflated and the central area depressed, with three to ten rounded or reniform foramina. The orifice is elongated, with paired condyles and four to six oral spines; the distal rim is often distinctly raised and hooded. There is slight ontogenetic thickening of the frontal shield, but no sign of a mucro. Avicularia are rare, occurring with a frequency of 1 : 8–10 zooids in parts of the colonies, although they are more frequent in other areas. They are fairly prominent, the rostra raised and truncate distally in well-preserved examples, rounded in others which appear to be worn. Generally, the majority is directed distally or distal-laterally; a few have a complete bar preserved. Vicarious avicularia are not present. Brood chambers are rare and badly preserved and only three have been seen. They are small and prominent, and the orifices of the brooding zooids are not dimorphic.

Although ancestrular regions are not present, a primary zone of change can be inferred in the holotype. By extrapolation of the existing series of zooids backward down the astogenetic gradient, it is inferred that the zooids belong approximately to the seventh or eighth generation from the origin of the colony. The increase in zooid length is expressed as a series: Lz 0·44, 0·46, 0·48, 0·51,

[1] Named after Mlle S. Pouyet, Université Claude Bernard, Lyon.

0·54, 0·58, 0·60 mm, ... The primary zone of repetition is established by the twelfth to fourteenth zooid generation from the hypothetical ancestrula. Increase in length of the orifice is expressed as a series: Lo 0·14, 0·16, 0·16, 0·18 mm, . . ., the maximum length being reached by the tenth to eleventh zooid generation. The zooids show the character of the orifice and frontal shield extremely well (see Pl. 4C); the condyles and spine bases, and the funnels between zooids are particularly clear. The zooids near the growing edge also show incipient brood chambers, the earliest appearing at the fifteenth zooid generation from the hypothetical ancestrula.

T. pouyetae differs from both *T. maçonnica* and *T. areolata* in its larger dimensions. It is very similar to *T. areolata*, but has a greater number of frontal foramina, raised distal borders to the orifices and shows no dimorphism in the orifices of brooding zooids.

The *Tremogasterina mucronata*-complex

The populations comprising '*T. mucronata*' appear to fall into three groups which are to some extent correlated in time and space. The eight species described by Canu & Bassler (1923, 1928a, 1928b) from Florida, the Gulf of Mexico and Brazil have been considered to fall within the range of *T. mucronata* (Smitt). These species appear to differ from each other in character states which are the result of astogenetic and ontogenetic stage, or in state of preservation of both fossil and Recent specimens. Great variation in size of zooids and orifices, number and degree of occlusion of foramina, number of spines and in size and shape of avicularia has been found in single colonies from the British Museum (Natural History) and United States National Museum Collections, which included states considered by Canu & Bassler to be specific (see Powell & Cook, 1967). Although some of the fossil populations seem to fall within *T. mucronata*, others, particularly some Miocene forms from North America, possess a correlation of character differences which relate them to the African and European fossil forms, and are therefore here treated as a separate population ('*T. miocenica*'). The Recent forms from the Mexican and Californian coast also show distinct character correlated differences, particularly in the size and shape of the orifices and avicularia, and are here considered to be a separate species, *T. subspatulata*.

a. *Tremogasterina mucronata* (Smitt)

Escharipora (?) *mucronata* Smitt, 1873 : 24, pl. 5, figs 113–115.
Tremogasterina mucronata (Smitt), Powell & Cook, 1967 : 9, pl. 1a, b.

Material examined. In addition to the specimens listed by Powell & Cook (1967), three specimens from the USNM collections have been examined (see Appendix, p. 141).

USNM *T. granulata* 'Albatross' Stn 3005; Fowey Light, 72 metres; *Tremogasterina* sp., 'Albatross' Stn. 2319, N. of Cuba.

Description (Pls 1B, C, 5C, 6E, F, Fig. 1E). Colony encrusting sponges, shell, Bryozoa, with unilaminar and bilaminar expansions and overgrowths. Zooids large, sometimes with more than one series of frontal septulae. Orifices with small lateral indentations and very small condyles and two to six oral spines. One to seven frontal foramina, placed in a central depression, becoming occluded wholly or in part during ontogeny. Suboral mucro often well developed. Avicularia very variable in size and shape, usually orientated distally. Rostra typically truncate with a distal expansion, but also acute or rounded, sometimes within one colony. Vicarious avicularia not generally common, but frequent in some colonies. Brood chambers large and wide.

Measurements (in mm).

Lz 0·60–1·00	Lo 0·17–0·25	Lov 0·24–0·35	Lr	0·25–0·60
lz 0·35–0·60	lo 0·14–0·24	lov 0·30–0·40	Lvic	0·60–0·80

Remarks. The very large range of variation among the fossil and Recent specimens assigned to *T. mucronata* was discussed by Powell & Cook (1967). The type-specimens of Canu & Bassler's species and much other material in the USNM collections has been re-examined. Some specimens (e.g. *T. ventricosa*) have a large number of small, acute avicularia and there is a tendency in some Miocene forms (e.g. *T. horrida* and *T. truncatorostris*) towards smaller zooids, but the ranges of

variation within colonies, particularly in the often fragmentary type-specimens, is extremely large. Each of the ranges for the twenty-two characters measured or assessed overlaps considerably among specimens, and it appears that ontogenetic and astogenetic differences are responsible in many cases for the very fine specific differences given by Canu & Bassler in the original descriptions. Several specimens were included in the analysis of populations (see Table 2), and these consistently clustered together. Osburn (1940 : 369) listed the records of Smitt (1873) and Canu & Bassler (1928a) in his paper on the Bryozoa of Porto Rico, but had no specimens in his collections. In a later paper, Osburn (1947 : 16) listed specimens from Venezuela which he assigned to *T. granalata*, *T. mucronata* and *T. malleolus* (see Appendix, p. 141).

A colony from the West Indies (BMNH 1931.5.2.6, Kingstown Harbour, St Vincent) has one vicarious avicularium; in addition, dimorphic zooids are present which have an extensive calcified frontal wall with a large, subdivided frontal foramen and frontal septulae. The distal part of the zooid is raised and extended, and the operculum is elongated with a long marginal sclerite and paired, partial medially directed sclerites in the distal part. The cuticle is thicker than that of the autozooidal opercula. The dimensions of these dimorphs, which are not frequent (four dimorphs among approximately 2000 autozooids) are: Lz 0·80–0·90 mm, lz 0·40 mm, L frontal 0·50 mm, Lo 0·28–0·34 mm.

b. '*Tremogasterina miocenica*' populations

Cribrilina miocenica McGuirt, 1941 : 67, pl. 2, figs 10–11.

Material examined. BMNH Chipola Formation, Middle Miocene, Florida.

Photographs of specimens from Givhans Bridge, Edisto River, Dorchester Co., S. Carolina, Miocene.

Description (Pl. 4A, B, Fig. 8B). Colony encrusting. Zooids small with flat frontal shields. Orifice with lateral indentations and two to four oral spines. One to four large frontal foramina. Avicularia large, raised, often randomly orientated, but regularly distal in parts of some colonies, rostra slightly expanded distally. Brood chambers prominent.

Measurements (in mm).

Lz 0·45–0·50	Lo 0·13–0·16	Lov 0·20–0·25	Lr 0·25–0·45
lz 0·25–0·40	lo 0·15–0·17	lov 0·20–0·29	

Remarks. McGuirt (1941) described specimens from the Middle Miocene of S. Louisiana. The dimensions and general appearance of the photographs of specimens from S. Carolina (on oyster shells) taken by Dr A. H. Cheetham are very similar. The avicularia in McGuirt's specimens were more frequent and more regularly distal in orientation. The specimens from the Chipola Formation (see Scolaro, 1968 : 174) show a great deal of variation in the size and orientation of the avicularia, and have a greater range in size of zooids.

Although larger than the zooids of *T. maçonnica*, the proportions of the calcified orifice and brood chamber and the form of the frontal areas are very similar. The similarity in relative size and orientation of avicularia between these specimens and the European Miocene *T. areolata* is also striking. At the same time the fossil specimens have much in common with both fossil and Recent specimens from the American region which are indistinguishable from *T. mucronata*.

c. *Tremogasterina subspatulata* Osburn

Tremogasterina granulata subspatulata Osburn, 1950 : 98, pl. 10, fig. 8.
Tremogasterina granulata magnipora Soule, 1959 : 25, text-fig. 3.

Material examined. USC Type-specimens of *T. g. subspatulata* Osburn; Clarion Id, Mexico, Velero Stn 137–34, 1.5.1934, 104 metres, Nos 1101, 7D11.

Type-specimens of *T. g. magnipora* Soule; Angel de la Guarda Is, Gulf of California, May 1957, 27–31 metres.

USNM *T. g. subspatulata*, Clarion Id.

DESCRIPTION (Pl. 6B, C, D). Colony encrusting sponges and shell, with unilaminar expansions. Zooids of encrusting parts fairly large, zooids of erect parts growing in 'verticillate' lateral rows having smaller dimensions. Orifices large with small lateral indentations and condyles and two to four evanescent spines (seen on very few zooids). No mucro. One to three frontal foramina, often occluded. Avicularia large, with acute rostra orientated distally. Rostra curved downward and finely serrate distally. Vicarious avicularia absent. Brood chambers wide.

MEASUREMENTS (in mm).

Lz 0·42–0·65	Lo 0·22–0·25	Lov 0·22–0·24	Lr 0·30–0·55
lz 0·29–0·34	lo 0·14–0·21	lov 0·30–0·36	

REMARKS. The material of *T. g. subspatulata* consists of eight unilaminar, sometimes curved fragments. The specimens of *T. g. magnipora* consist of three fragments, one encrusting shell, the others unilaminar and erect with serpulid tubes and sponges encrusting the basal wall. Together they comprise approximately 600 zooids. Brood chambers are present only in the specimens of *T. g. magnipora*. The characters of the two subspecies seem to be so similar that they may be considered to belong to a single taxon. There are small but consistent differences between them and the specimens assigned to *T. mucronata* from the other side of the Panamanian isthmus. The orifices are larger and the spine bases evanescent and rarely preserved. The avicularian rostra are consistently acute. Some specimens of *T. mucronata* which also exhibit verticillate growth, are, however, very similar in appearance. Until the entire *T. mucronata*-complex can be revised, using more plentiful material, the specimens from California and W. Mexico are here regarded as a distinct species.

Tremogasterina lanceolata Canu & Bassler

Tremogasterina lanceolata Canu & Bassler, 1928a : 48, pl. 13, fig. 9, text-fig. 6A. Powell & Cook, 1967 : 11.

MATERIAL EXAMINED. Listed by Powell & Cook (1967), see also Appendix, p. 141.

DESCRIPTION (Pl. 6A). Colony encrusting coral and other Bryozoa. Zooids large with small, terminal, elongated, sinuate orifices with lateral indentations and condyles large, and five to six spines. Three to eight small frontal foramina. Avicularia very elongated, rounded, orientated distally, with serrate rostra. Mandibles extending beyond the rostrum. Vicarious avicularia absent. Brood chambers prominent.

MEASUREMENTS (in mm).

Lz 0·50–0·85	Lo 0·16–0·18	Lov 0·24–0·28	Lr 0·30–0·55
lz 0·25–0·40	lo 0·10–0·13	lov 0·24–0·30	

REMARKS. *T. lanceolata* is here considered to be distinct from *T. mucronata*, although it is possible that specimens from other localities and depths might provide forms intermediate with some included in the *T. mucronata*-complex. The occurrence of two specimens of totally different appearance, from the same locality (Cuba, 146 metres), one assigned here to *T. mucronata* (see Appendix, p. 141), the other to *T. lanceolata* is, however, interesting. The zooids are very elongated, and the frontal foramina small, even early in ontogeny. The foramina are restricted to an elongated, depressed area, rather like that seen in some zooids of *T. pouyetae* (see Pl. 4C). The orifice is very small, with distinct condyles and a slightly sinuate appearance. The operculum which was figured by Canu & Bassler (1928a : text-fig. 6A) also differs considerably from that of both *T. mucronata* and *T. subspatulata*. The frontal septulae do not extend in a series completely round the distal border of the secondary calcified orifice. The avicularia are very long, and the rostra are rounded terminally, raised and serrate distally. The mandibles extend completely beyond the rostra and protrude either into the foramen complex of a distal zooid, or into a gap in the secondary calcification. This gap is presumably produced as the distal frontal shield calcifies, and is a direct result of the presence of the mandible of the proximal avicularium. Similar obstruction of calcification by mandibles has been observed in *T. subspatulata* and in isolated zooids of 'verticillate' colonies of *T. robusta* (see p. 133).

Tremogasterina robusta (Hincks)

Lepralia robusta Hincks, 1884 : 360, pl. 13, fig. 4.
Tremogasterina robusta (Hincks), Powell & Cook, 1967 : 12, pl. 1, figs c, d, text-figs 1–4. Powell, 1967 : 166.

Material examined. In addition to that listed by Powell & Cook, 1967 (see Appendix, p. 143). BMNH, Perin Is, Aden, 1966.2.24.1 and 1966.9.2.2, 15 metres.

Gulf of Oman, 1972.7.1.13–16, 18 metres.

? Pleistocene, Givan Peninsula, Red Sea, Reef Limestone, BMNH L51638, 1975.10.4.1, on *Saccostrea* cf. *cucullata* (Born).

Description (Pls 5E, 8B, C, Fig. 1D). Colony encrusting oyster shell and coral, zooids very large. Orifice with lateral indentations and condyles and two (occasionally three) spines. One to three frontal foramina, frequently only one present, tripartite at first, often occluded early in ontogeny. Avicularia large, with asymmetrically curved, slightly spathulate or acute mandibles, orientated distally. Vicarious avicularia rare. Brood chambers not prominent.

Measurements (in mm).

Lz 0·60–1·20	Lo 0·24–0·30	Lov 0·20–0·30	Lr 0·40–0·70
lz 0·40–0·65	lo 0·16–0·20	lov 0·30–0·40	Lvic 0·40–0·60

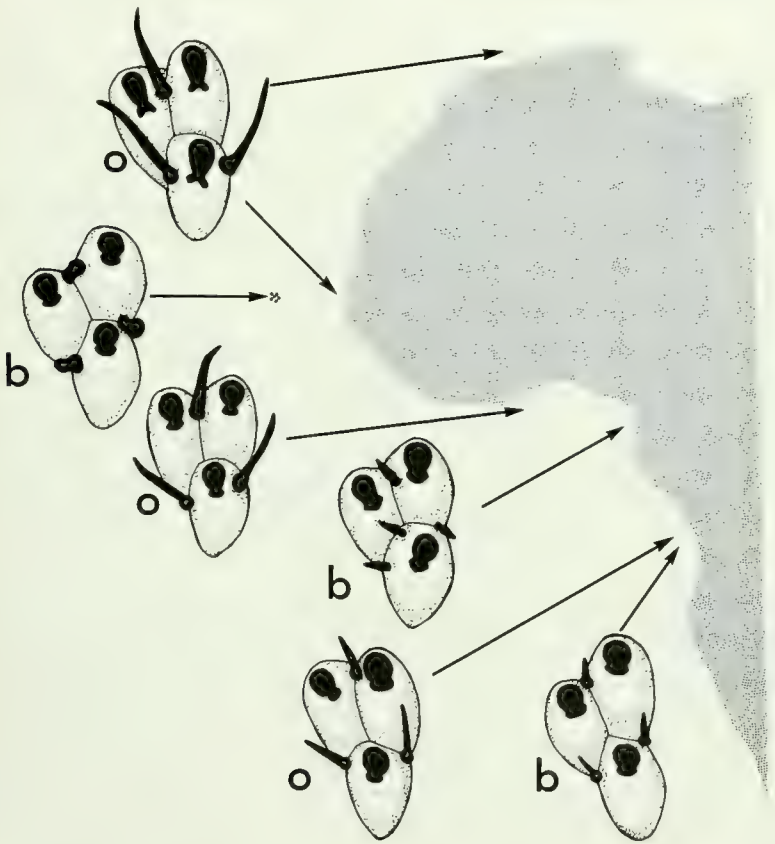

Fig. 7 *T. oranensis* (Waters) and *T. brancoensis* (Calvet). Correlation of orifice shape with avicularium size, shape and orientation; showing distinction in character states between the two 'typical' northern populations of both species, and convergence of states with progressive southerly distribution. (o) *T. oranensis*; (b) *T. brancoensis*.

Remarks. Recent specimens from the Red Sea have been described in detail by Powell & Cook (1967). Approximately 500 Tertiary oyster and coral specimens in the Palaeontology Department collections at the British Museum (Natural History) have been examined. Many of these show remains of bryozoan colonies, but only one has been found with recognizable colonies of *Tremogasterina* encrusting it. The fossil (? Pleistocene) specimens consist of two colonies encrusting the outer surface of an oyster shell and together comprise approximately 1300 zooids. As many as three laminae are present, most of the overgrowth layers being worn. The zooids are distinctly smaller than those of Recent specimens and show large, chambered distal and lateral septulae and fourteen to twenty well-marked frontal septulae which have developed in many cases into areolae. Few joint funnels have been developed and generally there is little frontal thickening. Many zooids have no apparent frontal foramina, but an equal number have one, oval foramen. The orifices resemble those of Recent *T. robusta* in being slightly elongated, with distinct lateral indentations and condyles; scars of two oral spines are present in three zooids. The avicularia are slightly smaller than those of Recent Red Sea specimens, and the rostra are neither curved nor expanded distally, but acute. Only one, broken, brood chamber has been preserved and vicarious avicularia are apparently absent.

The Tremogasterina oranensis–brancoensis-complex

Examination of material from the regions extending from the north-western African coasts to Angola and the Congo has shown that the populations of these two species exhibit a similarity in character which increases with southerly distribution. The populations do not become indistinguishable, however, and at the extremes of their ranges of variation are completely distinct. They are therefore treated separately.

Preliminary analysis of populations of specimens found in accumulated bottom samples from the Congo and Angola coasts from the Collections of the Muséum Royale de l'Afrique Centrale, and consequent re-examination of material from West Africa, including new collections from Ghana, has shown that *T. oranensis* and *T. brancoensis* are not exclusively allopatric species (cf. Cook, 1964 : 20), and that a third form is present. All three show a progressive degree of similarity in characters associated with the orifice and avicularia. These similarities are also correlated with distribution, and a species complex appears to be present along the north-west to south-west African coasts which requires further investigation.

A summary of the preliminary analysis is given in Fig. 7. Geographically, the Cape Verde Island and Oran-to-Guinea populations comprise two distinct species, *T. brancoensis* and *T. oranensis* respectively. Specimens from the Bay of Biafra, previously assigned to *T. brancoensis*, may be specifically distinct from those from the Cape Verde Islands, but those from the Congo region appear to be intermediate in character. Accompanying specimens of *T. oranensis* from the Congo region, however, also show characters which approach those of the non-typical populations of *T. brancoensis*.

The correlated changes are as follows. In *T. brancoensis* the sinus is rounded in the Congo form, and distinctly elongate and even more rounded in the Bay of Biafra form. The short rounded or oval interzooidal avicularia of the typical population are acute in the other forms, and their orientation becomes more regularly distal. At the same time, vicarious avicularia, which are frequent and conspicuous in specimens from the Cape Verde Islands, become very rare in the Bay of Biafra form, and are apparently absent in colonies from the Congo region. In *T. oranensis*, orifices of colonies from the Congo area show a considerable decrease in the length of the distal part in comparison with the length of the sinus. Concurrently, the proximal edge of the orifice changes from concave in specimens from Senegal to straight in those from Ghana, and to slightly convex in the Congo populations. These orifices are very similar in shape to those of *T. brancoensis* from the same area. The size and shape of the avicularia of *T. oranensis* show a similar series of changes, becoming progressively smaller and less hooked with southerly distribution; until the avicularia of the Congo and Angola populations of both *T. oranensis* and *T. brancoensis* are very alike in size, shape and orientation.

In the absence of fossil specimens, it is impossible to judge whether or not these progressive sequences of correlated differences are indicators of convergence or divergence, or of completely independent environmentally induced reaction.

Tremogasterina oranensis (Waters)

Lepralia oranensis Waters, 1918 : 101, pl. 12, figs 11–13.
Cleidochasma oranense (Waters) Cook, 1964 : 17, pl. 2, fig. 3, pl. 3, fig. 2, text-fig. 6A–B. 1968 : 198, pl. 8, fig. h.

Material examined. In addition to that listed by Cook (1964, 1968) material is from bottom samples from Loanda, Congo and Malembe, Angola, from the MAC Collections.

Description (Pls 5F, 7C, D, 8E, F, Figs 1C, 7). Colony encrusting almost any available substratum, often erect and tubular, with multilaminar overgrowths. Zooids small, orifices elongated, with lateral indentations and very large lateral condyles, delineating a proximal sinus which may be concave, straight or convex proximally. There are four oral spines and one to four frontal foramina present very early in the ontogeny, usually occluded later. Avicularia large, with an elongated acute rostrum and a hooked mandible, which is hinged to a complete bar. Vicarious avicularia occasionally present. Brood chambers prominent at first, rapidly becoming immersed by secondary calcification.

Measurements (in mm).
Northern specimens:
Lz 0·35–0·52 Lo 0·20–0·24 Lov 0·18–0·22 Lr 0·30–0·45
lz 0·30–0·52 lo 0·11–0·14 lov 0·20–0·23
Ghanaian specimens:
Lz 0·40–0·55 Lo 0·18–0·20 Lov 0·19–0·22 Lr 0·25–0·40
lz 0·38–0·48 lo 0·12–0·14 lov 0·21–0·24 Lvic 0·50–0·65
Angolan specimens:
Lz 0·45–0·55 Lo 0·19–0·21 Lov 0·20–0·21 Lr 0·10–0·30
lz 0·35–0·42 lo 0·14–0·15 lov 0·20–0·24

Remarks. Examination of additional material collected alive from Ghana has revealed that the early ontogeny of the frontal shield is umbonuloid. The species was previously (see Cook, 1964) assigned to *Cleidochasma*, a genus which has a similar form of orifice, spines and brood chambers. *C. protrusum*, the type-species of *Cleidochasma*, and the widely distributed *C. porcellanum*, both have a cryptocystidean type of frontal wall ontogeny. In addition to its umbonuloid ontogeny, *T. oranensis* possesses all other structures characteristic of *Tremogasterina* as used here.

The earliest stages of zooidal development show an uncalcified anasciform frontal wall, above which develops a typically umbonuloid calcified frontal shield as described on p. 107. The fusion of the distal lateral processes delineates a large elongated oval, the future orifice, and an equally large foramen proximally. The operculum is fully differentiated before this stage, after which the lateral indentations and large condyles are formed, and the proximal foramen becomes rapidly divided and reduced to three to four small irregular or lunate foramina. The occlusion of the foramina follows rapidly (few zooids more than one series proximal to the growing edge show any sign of a foramen). In specimens cleaned with eau de javel, small foramina may still be seen, however, in zooids which have quite thick secondary calcification, and it is probable that, although generally covered by cuticle, and occluded by calcification, some foramina continue to remain uncalcified (see Pl. 8F), or even open. Zooids surrounding the ancestrula in the primary zone of astogenetic change are of interest in that they possess several foramina throughout their ontogeny, and greatly resemble zooids at the same astogenetic stage seen in *T. spathulata* and *T. robusta* (see p. 106, and Fig. 1).

Tremogasterina brancoensis (Calvet)

Lepralia brancoensis Calvet, 1906 : 159, 1907 : 410, pl. 27, figs 7–9.
Cleidochasma brancoense (Calvet), Cook, 1964 : 19, pl. 2, fig. 4, pl. 3, fig. 1, text-fig. 6C–D. 1968 : 199.

Material examined listed by Cook (1964, 1968), see also Appendix, p. 142.

Description (Pls 7A, B, 8D, Fig. 7). Colony encrusting shell, hydroids, rising in erect bilaminar branches, with multilaminar overgrowth. Orifices with lateral indentations and condyles delineating a rounded proximal sinus. Two evanescent spines and one to two small frontal foramina present at earliest ontogenetic stages, the foramina becoming rapidly occluded. Avicularia small, randomly orientated, with a rounded rostrum (in 'typical' form) and mandible hinged to a complete bar. Vicarious avicularia large, spathulate, sometimes common. Brood chambers prominent at first, rapidly immersed by secondary calcification.

Measurements (in mm).

Cape Verde Islands specimens:

Lz 0·45–0·75	Lo 0·20–0·22	Lov 0·20–0·24	Lr 0·10–0·25
lz 0·40–0·53	lo 0·14–0·16	lov 0·28–0·30	Lvic 0·40–0·65

Bay of Biafra specimens:

Lz 0·55–0·80	Lo 0·22–0·26	Lov 0·20–0·25	Lr 0·05–0·16
lz 0·35–0·47	lo 0·14–0·16	lov 0·25–0·28	Lvic 0·40–0·60

Angolan specimens:

Lz 0·40–0·53	Lo 0·18–0·20	Lov 0·18–0·22	Lr 0·07–0·14
lz 0·32–0·45	lo 0·14–0·16	lov 0·22–0·25	

Remarks. The series showing the frontal shield ontogeny is not as complete in *T. brancoensis* as in *T. oranensis*, but it is umbonuloid. The proximal foramina are small and evanescent, and rapidly occluded by calcification. One distinctive character of *T. brancoensis* is the relatively random (most frequently lateral) orientation of the interzooidal avicularia. In the 'typical' population, the difference between the mandible shapes of the interzooidal and vicarious avicularia is also striking. *T. brancoensis* also differs from other species in the bilaminar habit. Like those of *T. oranensis*, however, the erect branches are covered by several layers of overgrowth during the later astogenetic stages of colony growth.

As in *T. mucronata*, zooids occasionally develop more than one series of frontal septulae, especially in areas of irregularity in overgrowths.

Tremogasterina celleporoides (Busk)

Lepralia celleporoides Busk, 1884 : 142, pl. 17, fig. 4.
Tremogasterina celleporoides (Busk) Canu & Bassler, 1929: 118, pl. 12, figs 1–6; Harmer, 1957: 659, pl. 49, figs 18–21.

Material examined. Includes all specimens listed by Harmer, 1957 (see also Appendix, p. 143), and BMNH, China Sea, 1962.2.20.7.

Description (Pls 1A, D, 2, 5D, 8A). Colony encrusting coral and shell, with unilaminar and tubular expansions. Zooids fairly large. Orifices wide, with two to three evanescent spines and small condyles. One to two large frontal foramina, often one tripartite foramen, not often occluded. Avicularia large, with a spathulate mandible orientated randomly. Vicarious avicularia common, often very large. Brood chambers wide.

Measurements (in mm).

Lz 0·50–0·70	Lo 0·19–0·22	Lov 0·20–0·30	Lr 0·25–0·40
lz 0·30–0·45	lo 0·18–0·20	lov 0·24–0·36	Lvic 0·60–0·70

Remarks. *T. celleporoides* forms large, erect colonies with anastomosing, tubular expansions which are multilaminar. It has been described in detail by both Busk (1884) and Harmer (1957).

Tremogasterina spathulata (Canu & Bassler)

Hiantopora spathulata Canu & Bassler, 1929 : 116, pl. 11, figs. 13, 14.
Arachnopusia spathulata (Canu & Bassler), Harmer, 1957 : 657, pl. 68, figs 22, 23, 25, 31.
Tremogasterina spathulata (Canu & Bassler), Powell & Cook, 1967 : 11.

MATERIAL EXAMINED. In addition to that listed by Powell & Cook (1967), see also Appendix, p. 143.

BMNH, Ghardaqa, Red Sea, 1965.9.4.1; China Sea, 1962.2.20.8; South China Sea, DG8, 'Dampier' sample; Aldabra Id, 1971.3.16.1A and 1972.6.1.11; Mahé, Seychelles, 1975.9.24.4.

Professor D. A. Brown Coll. Pliocene, Midway Id, reef, Hole R103–5′, No. 152.

Mr R. Day Coll. Recent, Heron Id, south Gt Barrier Reef.

DESCRIPTION (Pl. 5A, Figs 1B, 8A). Colony encrusting shell and coral. Zooids small. Orifice wide, with small lateral indentations and four to five spines. Two to twenty frontal foramina, lunate or irregular, becoming surrounded by funnels of calcification. Avicularia with mandibles expanded and truncate distally, or rounded. Rostra orientated distally or randomly. Vicarious avicularia sometimes present. Brood chambers wide.

MEASUREMENTS (in mm).

Lz	0·40–0·56	Lo	0·10–0·17	Lov	0·19–0·23
lz	0·30–0·40	lo	0·12–0·14	lov	0·26–0·30
Lr	0·10–0·24				
Lvic	0·40–0·50				

REMARKS. The diversity in characters among samples of *T. spathulata* may be related to their wide geographical range, but the correlation is not directly connected with either geographical or bathymetrical distribution. Colonies are usually small and inconspicuous, and some of the samples (e.g. South China Sea, No. 38 and Midway Is, No. 37) consist of one or two small fragments only. The colonies from the Seychelles are slightly larger and differ consistently in several characters. The zooids have a prominent apertural bar with a low mucro and usually only two to four frontal foramina, which are surrounded by a slightly raised, wide funnel of calcification. The avicularia have raised, rounded rostra, quite unlike the truncate, expanded form of most of the other specimens. The general aspect of these colonies is remarkably similar to that of *T. maçonnica*, and quite unlike that of the specimens from the Red Sea and Aldabra, which are nearest geographically. Vicarious avicularia are not common and have been found in the samples from the Red Sea and Australia only.

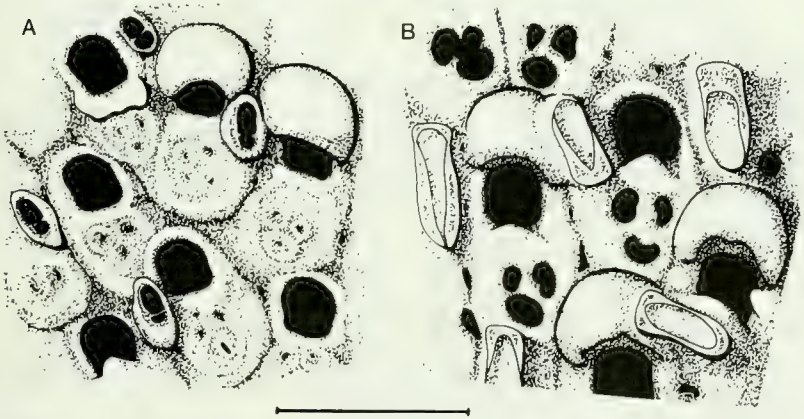

Fig. 8 Recent and fossil *Tremogasterina*. (A) *T. spathulata* (Canu & Bassler), Recent, Seychelles, BMNH, 1975.9.24.4. Zooids, brood chambers and avicularia at a late stage of ontogenetic calcification. Note the unusually small number of frontal foramina, the rounded avicularian rostra and the general similarity with the zooids of the Eocene *T. maçonnica* (see Pl. 3C, D and cf. *T. spathulata*, Pl. 5A. (B) '*T. miocenica*', Miocene, Chipola Formation, Florida, BMNH. Zooids, brood chambers and avicularia at a late stage of ontogenetic calcification. Note the general similarity with the zooids of *T. areolata* (see Fig. 6A) particularly in the incorporation of avicularian subrostral chambers in the calcification of the brood chambers. Scale = 0·50 mm.

Tremogasterina perplexa Cook

Tremogasterina perplexa Cook, 1967 : 336, fig. 8. 1968 : 173.

MATERIAL EXAMINED. UMC, Holotype, 'Atlantide' Stn 146, 9°24′ N, 14°48′ W, 19.4.46, 50–51 metres, 107 F, on shell.

BMNH, 'Calypso' Stn 25, 4°36′5″ N, 1°31′ W, 24.5.56, 50 metres, C 1OU, 1973.3.22.27, on stones.

DESCRIPTION (Pls 1E, 7E, Fig. 1A). Colony encrusting shell and stones. Zooids small, orifices elongated with lateral indentations and six long spines. Seven to fifteen frontal foramina, each often with a unilateral process, secondarily calcified as thickened funnel-shaped expansions, eventually forming blocks of calcifications. Frontal suboral mucro often enlarged. Secondary calcification forming a ridge or hollow, mucronate process, often obscuring the frontal foramina. Avicularia absent. Brood chambers small.

MEASUREMENTS (in mm).

Lz 0·40–0·65	Lo 0·10–0·13	Lov 0·20–0·25
lz 0·26–0·36	lo 0·08–0·10	lov 0·20–0·27

REMARKS. *T. perplexa* was originally described from a single colony. The additional specimens from the 'Calypso' Collection are at an earlier stage in ontogeny, and many zooids have not developed the massive frontal ridges of secondary calcification. These colonies encrust small stones; one consists of twelve zooids, including the ancestrular region, the other is larger, consisting of 120 zooids, some with brood chambers.

The spines are very long, with a sigmoid curve and cuticular base. The opercular sclerite is very long proximally and the two ends extend into the frontal membrane below the edge of the secondary calcified orifice.

T. perplexa differs from all other species of *Tremogasterina* in the complete absence of avicularia. Its known distribution now extends from Guinea to the Ghanaian coast.

Tremogasterina musaica[1] sp. nov.

MATERIAL EXAMINED. HOLOTYPE, BMNH, off Ghana, 'deep water' (>50 metres), 1970.2.8.9.

Paratypes, S36, bottom sample, south west of Tema, Ghana, probably from >50 metres, 1973.3.22.31.

DESCRIPTION (Pls 1F, 5B). Colony encrusting calcareous accretions and worm-tubes, multilaminar. Zooids small, orifices elongated, with a rounded proximal sinus and distinct lateral indentations and condyles, and four to six oral spines. Eight to fifteen small, lunate frontal foramina. Secondary calcification forming funnels, followed by blocks of calcification. Avicularia small, interzooidal only, with acute mandibles directed distally and slightly laterally and hinged to a complete bar. Brood chambers fairly prominent.

MEASUREMENTS (in mm).

Lz 0·40–0·50	Lo 0·15–0·17	Lov 0·20–0·24	Lr 0·14–0·20
lz 0·30–0·38	lo 0·12–0·13	lov 0·22–0·30	

REMARKS. The orifice of *T. musaica* has a distinct rounded sinus, similar to that of *T. brancoensis*, from which it differs in its colony form, frontal calcification, number of spines and lack of vicarious avicularia. It also differs from *T. spathulata* in the shape of the avicularia, and from both *T. spathulata* and *T. perplexa* in the shape of the orifice.

The blocks of calcification surrounding the foramina resemble those found in the later ontogenetic stages of *T. perplexa*, but are not accompanied by the development of large ridges or mucronate processes. The succession of ontogenetic changes in both species is as follows. Lunate foramina become surrounded, either singly or in groups, by funnel-shaped pits with smooth calcification and raised borders (see *T. perplexa*, Pl. 1E). These thicken frontally, and eventually become closely apposed, forming blocks. The marginal frontal septulae apparently remain

[1] Musaicus (L) – mosaic, referring to the appearance of the calcified frontal shield.

capable of transporting nutrients to the hypostegal coelomes during these ontogenetic changes, which are similar to those found in *Exechonella*. Somewhat similar blocks of calcification were reported by Canu & Bassler (1920 : 312) in *Arachnopusia vicksburgica* (see p. 000). If this species proves to be referable to *Tremogasterina* it differs in the size of the zooids, shape of orifice, and apparent absence of spines.

Specimens from the S36 bottom sample include a series of species not generally found in Ghana from less than 50 metres depth. The area south-west of Tema is one where an embayment from deeper water encroaches landward. The material from these sediments is generally, but not exclusively, dead. Much of it is fragmentary and may have been transported. Species found in these samples include *Cupuladria doma*, *Aptonella violacea* and *Cleidochasma rotundorum*.

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Summaries in French and German

Le developpement historique de la conception generale de genre *Tremogasterina* a été discuté, et nous donnons ici un aperçu des correlations des caractères que nous considerons comme typiques de genre çi-dessus. La nomenclature et les affinités du *Tremogasterina* et *Poricella* sont examinés. Nous décrivons ici les régions ancestrulares et l'astogénie des zooides, les aviculaires et les chambres d'incubation ('ovicelles'). L'ontogènese du bouclier anterieur suit le modèle umbonuloide, dans lequel le pli externe, basiquement calcifié, se developpe frontalement envers le mur et l'orifice primaire, qui sont non-calcifiés. Les chambres d'incubation dans *Tremogasterina* sont apparement les modifications des bourgeons intra-zooidales et frontales. Leur ontogénie est décrite et comparée avec celle découverte récemment dans d'autres genres. La nature de l'ontogénie du bouclier frontal et la convergence de traits morphologiques avec les formes cryptocystidiennes sont pareilles à celle découverte déjà dans Adeonidae at Adeonellidae. L'analyse des populations indique que deux traits divergents dans la zooide et la structure de la colonie ony pu évoluer depuis le Paléocène. Quinze espèces nominales ou populations sont décrites, dont deux sont considerées nouvelles, et leur distribution dans le temps et l'espace est discutée. Des problèmes de reconnaissance et d'interpretation, particulièrement des échantillons fossiles, sont discutes et des investigations nouvelles ont été suggerées qui puissent fournir des solutions nouvelles.

Die historische Entwicklung des allgemeinen Konzepts der Merkmale der Gattung *Tremogasterina* wird diskutiert, und die Gegenwärtig für diese Gattung als typisch angesehenen Merkmalskorrelationen werden zusammengefasst. Die Nomenklatur und die Beziehung der Gattungen *Tremogasterina* und *Poricella* zueinander werden ebenfalls diskutiert. Die Anzestrularregion und die Astogenie der Zooezien, Avikularien und Brutkammern ('Ovizellen') werden beschrieben. Die Ontogenie des Frontalschildes folgt dem umbonuloiden Muster, bei dem sich eine äussere, basal verkalkte Falte über der primären unverkalkten Frontalwand und dem Orificium entwickelt. Die Brutkammern von *Tremogasterina* sind offenbar modifizierte interzooezielle Frontalknopsen. Inre Ontogenie wird beschrieben und mit der in jüngster Zeit bekanntgewordenen anderer Gattungen verglichen. Die Art der Ontogenie des Frontalschildes und die Konvergenz der morphologischen Merkmale die Formen cryptocystidien ist den bei den Adeonidae und Adeonellidae gefundenen Verhältnissen analog. Auf Grund der Populationsanalysen erscheint es möglich, dass sich seit dem Paläozän zwei divergierdene Trends der Zooezien- und Kolonie-

strukturen entwickelt haben. Es werden fünfzehn nominelle Arten oder Populationen beschrieben, zwei davon neu, und ihre zeitliche und räumliche Verbreitung wird diskutiert. Die Probleme des Erkennens und der Interprätation, besonders von fossilen Exemplaren, wird diskutiert, und weitere mögliche Wege zur Klärung werden vorgeschlagen.

Appendix

The following records of species of *Tremogasterina* have been noted; those plotted on Maps 1 and 2 are marked*.

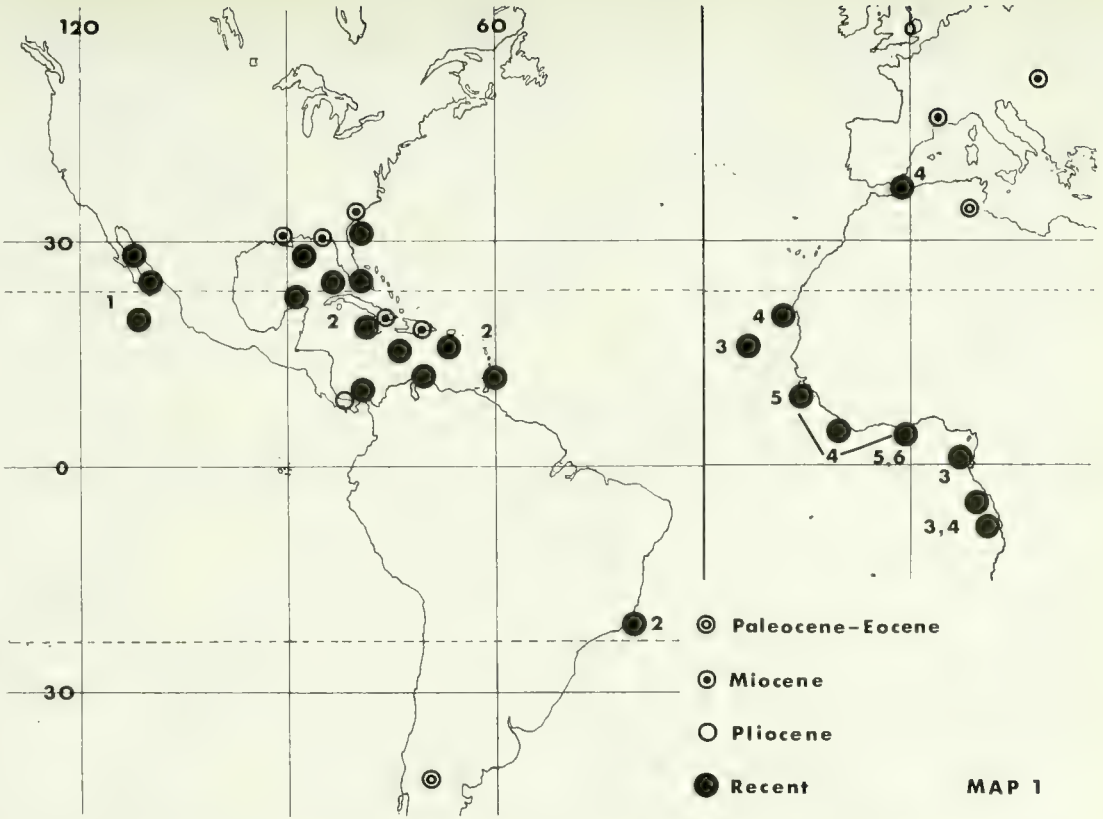
Locality data		Reference	BMNH	Name
Paleocene				
*Argentina	Approx. 39° S, 68° W, Barranca del Jaguel, Neuquén Province	Canu, 1911		*T. problematica*
Eocene				
*Tunisia	Approx. 34°30′ N, 9°00′ E, Djebel Blidji ver le Nord, massif ouest de Gafsa	Canu, 1904		*T. maçonnica*
Miocene				
*Austria	Baden	Reuss, 1874		*T. areolata*
*France	Saint Jean and Nezignan l'Evêque, Hérault			*T. pouyetae*
*Florida	Jackson Bluff, Ocklocknee R., 25 miles SW of Tallahassee	Canu & Bassler, 1923 (*T. horrida*)		*T. mucronata*
Florida	Chipola formation		BMNH	'*T. miocenica*'
*S. Carolina	Givhans Bridge, Edisto R., Dorchester Co.	A. H. Cheetham Coll.		'*T. miocenica*'
*Louisiana	Core at 7989 ft, Acadia Parish	McGuirt, 1941 (*C. miocenica*)		'*T. miocenica*'
*Cuba	Santiago	Canu & Bassler, 1923 (*C. cuspidata*)		*T. mucronata*
*San Domingo	Bowden horizon	Canu & Bassler, 1923 (*T. truncatorostris*)		*T. mucronata*
Pliocene				
*Panama	Minnitimmi Creek, Bocas Id, Almirante Bay	Canu & Bassler 1928a (*T. granulata, T. malleolus, T. sparsiporosa*)		*T. mucronata*
*Midway Id	Reef hole, 103·5 ft, No. 152	D. A. Brown Coll.		*T. spathulata*
? *Pleistocene*				
*Red Sea	17°06′ N, 42°21′ E, Gizan Peninsula		1975.10.4.1	*T. robusta*
Recent				
*W. Mexico	18°20′05″ N, 114°44′40″ W, 58 metres	Osburn, 1950 (*T. g. subspatulata*) and USNM		*T. subspatulata*
Lower California	Angeles Bay	Osburn, 1950 (*T. g. subspatulata*) and USNM		*T. subspatulata*
*Bay of California	28°45′30″ N, 112°23′ W, 36–40 metres and 11 other Stations, 9–84 metres	Soule, 1959 (*T. g. magnipora*)		*T. subspatulata*

Locality data		Reference	BMNH	Name
*Bay of California	Espiritu Santo Is, 18–44 metres	Soule, 1959 (*T. g. magnipora*)		*T. subspatulata*
Bay of California	25°2′45″ N, 110°43′30″ W, 38 metres, Albatross Stn 3005	USNM		*T. subspatulata*
*Gulf of Mexico	Alacran Reef, Campeche Bank		1961.11.2.41	*T. mucronata*
*Panama	9°36′9″ N, 79°40′08″ W, North of Porto Bello		1971.3.12.3	*T. mucronata*
*Gulf of Mexico	28°44′ N, 85°16′ W, 110 metres, Albatross Stn 2404	Canu & Bassler, 1928a (*T. granulata*, *T. malleolus*) USNM		*T. mucronata*
Gulf of Mexico	Approx. 25° N, 83 °W, W. of Tortugas, 66 metres	Smitt, 1873		*T. mucronata*
Gulf of Mexico	23°10′37″ N, 82°20′06″ W, 195 metres, Albatross Stn 2319	USNM		*T. mucronata*
*N. of Cuba	23°10′39″ N, 82°18′48″ W, 258 metres, Albatross Stn 2320	Canu & Bassler, 1928a and USNM	1932.3.7.61	*T. lanceolata*
N. of Cuba	Havana, 146 metres		1911.10.1.1713	*T. lanceolata*
N. of Cuba	Havana, 146 metres		1911.10.1.1692	*T. mucronata*
Gulf of Mexico	25°04′50″ N, 80°15′10″ W, 102·5 metres, Albatross Stn 2639	Canu & Bassler 1928a (*T. granulata*)	1932.3.7.44	*T. mucronata*
*Off Georgia	31°31′ N, 79°05′ W, 506 metres, Albatross Stn 2672	Canu & Bassler, 1928a (*T. ventricosa*)		*T. mucronata*
*E. Florida	Fowey Light, 15 miles S. of Miami, 73 metres	Canu & Bassler, 1928a (*T. granulata*) and USNM		*T. mucronata*
*Jamaica	Discovery Bay, 61 metres		1965.8.2.1, 2 1966.1.6.1	*T. mucronata*
*W. Caribbean	17°43′40″ N, 75°38′25″ W, 95 metres, Albatross Stn 2136	Canu & Bassler, 1928a (*T. malleolus*)		*T. mucronata*
Gulf of Venezuela	11°30′ N, 71° W, 71 metres	Osburn, 1947 (*T. mucronata*)		*T. mucronata*
Gulf of Venezuela	12°09′ N, 70°31′ W, 71 metres	Osburn, 1947 (*T. malleolus*)		*T. mucronata*
*Gulf of Venezuela	12°30′ N, 70° W, 129 metres	Osburn, 1947 (*T. granulata*)		*T. mucronata*
*E. Caribbean	18°30′ N, 66°18′50″ W, 146–219 metres, Caroline Stn 104	USNM 9766		*T. mucronata*
E. Caribbean	St Thomas		1840.10.23.82	*T. mucronata*
E. Caribbean	Kingstown Harbour, St Vincent		1931.5.2.6	*T. mucronata*
E. Caribbean	Grenada, 211 metres		1911.10.1.1698	*T. mucronata*
*Brazil	21°48′ S, 40°03′ W, 128 metres	Canu & Bassler, 1928b (*T. malleolus*)		*T. mucronata*
*Cape Verde Is	15°16′34″ N, 23°47′44″ W, 55–60 metres, Calypso Stn 24	Cook, 1964	1964.9.1.41–43	*T. brancoensis*
Cape Verde Is	15°16′30″ N, 23°47′31″ W, 50–65 metres, Calypso Stn 26	Cook, 1964	1964.9.1.44	*T. brancoensis*

Locality data		Reference	BMNH	Name
*Mauritania	21°05′ N, 17°14′ W, 43–45 metres, Calypso Stn 1			*T. oranensis*
Mauritania	22°19′ N, 17°05′ W, 62 metres, Galathea Stn 4			*T. oranensis*
Mauritania	Cap Blanc, 20–30 metres	Canu & Bassler, 1928c		*T. oranensis*
Mauritania	Cap Blanc, 20–64 metres		1921.5.23.7 1927.10.30.11	*T. oranensis*
Senegal and Guinea	20 Stations, Marche-Marchad Coll. 34–100 metres	Cook, 1964	1964.9.1.37 1970.8.10.9A	*T. oranensis*
Senegal and Guinea	10°22′ N, 16°22′ W, 41–55 metres, Atlantide Stn 44	Cook, 1968		*T. oranensis*
Senegal and Guinea	9°23′ N, 15°07′ W, 30–34 metres, Atlantide Stn 45	Cook, 1968		*T. oranensis*
*Senegal and Guinea	9°27′ N, 14°48′ W, 50–51 metres, Atlantide Stn 146	Cook, 1967 and Cook, 1968		*T. oranensis* *T. perplexa*
Senegal and Guinea	9°20′ N, 14°15′ W, 32 metres, Atlantide Stn 145	Cook, 1968		*T. oranensis*
*Liberia	5°06′ N, 9°34′ W, 78 metres, Atlantide Stn 60	Cook, 1968		*T. oranensis*
Liberia	Petit Tahou	Cook, 1964		*T. oranensis*
Ghana	4°43′ N, 1°41′ W, 46 metres, Atlantide Stn 75	Cook, 1968		*T. oranensis*
*Ghana	4°36′05″ N, 1°31′ W, 50 metres, Calypso Stn 25	Cook, 1967	1973.3.22.27	*T. perplexa*
Ghana	5 Stations, Achimota Coll., 0–65 metres	Cook, 1964	1964.9.1.34A, 35, 36 and 1966.1.10.1	*T. oranensis*
Ghana	Off Tema, 50 metres		1970.2.8.9pt 1973.3.22.31	*T. musaica*
Ghana	5°37′ N, 0°38′ E, 28–50 metres, Atlantide Stn 85	Cook, 1968		*T. oranensis*
*Oran	92–118 metres,	Barroso, 1925		*T. oranensis*
Oran	97 metres	Waters, 1918		*T. oranensis*
*Bay of Biafra	0°25′ N, 9°01′ E, 73 metres, Calypso Stn 45	Cook, 1964	1964.9.1.38–40	*T. brancoensis*
Bay of Biafra	2°03′ S, 9°01′ E, 49–50 metres, Atlantide Stn 123	Cook, 1968		*T. brancoensis*
*Congo	M'Vassa		1973.3.22.34	*T. brancoensis*
Congo	Landana		1973.3.22.33	*T. oranensis*
*Angola	Malembe		1973.3.22.32 1973.3.22.35	*T. oranensis* *T. brancoensis*
Angola	Cabinda	Cook, 1968		*T. brancoensis*
Angola	Ombrizette	Cook, 1968		*T. brancoensis*

Locality data		Reference	BMNH	Name
*Red Sea	Ghardaqa	Harmer, 1957	1961.10.30.9, 1965.9.4.1	*T. spathulata*
*Red Sea	Eilat		1965.8.30.2	*T. robusta*
*Red Sea	Khor Dongola	Waters, 1909		*T. robusta*
*Red Sea	Gorgussum and Sheikh Said, Massawa, 14·5 metres	Powell & Cook, 1967	1965.2.4.9,11–14, 1965.8.8. 6–9, 1970.1.4.1	*T. robusta*
Red Sea	Mersa ar-Rakiyai		1964.7.24.1	*T. robusta*
Red Sea	E. of Madote Id, 18–36 metres	Powell, 1967		*T. robusta*
*Gulf of Aden	Perin Is, Aden, 15 metres		1966.2.24.1, 1966.9.2.2.	*T. robusta*
*Indian Ocean	9°22′35″ S, 46°14′41″ E, Aldabra Id reef		1971.3.16.1A 1972.6.1.11	*T. spathulata*
*Indian Ocean	4°30′S, 55°30′ E, Mahé, Seychelles		1975.9.24.4	*T. spathulata*
*Indian Ocean	Seychelles, 22 metres		1882.10.18. 34–41 pt.	*T. robusta*
Persian Gulf			1889.7.1.5338, 5348	*T. robusta*
*Gulf of Oman	26°10′ N, 56°10′ E, 18 metres		1972.7.1.13–16	*T. robusta*
*Ceylon	Gulf of Manaar	Thornely, 1905	1936.12.30.42	*T. robusta*
*Burma	12°30′ N, 98°30′ E, Mergui	Hincks, 1884		*T. robusta*
*S. China Sea	5°59′ N, 112°35′ E 430 metres		DG 8 Dampier	*T. spathulata*
*S. China Sea	23°32′ N, 119°35′ E		1962.2.20.8	*T. spathulata*
			1962.2.20.7	*T. celleporoides*
*W. Flores	8°30′ S, 119°00′ E, 0–40 metres, Siboga Stn 50	Harmer, 1957	1961.10.30.11	*T. celleporoides*
W. Timor	Hangsisi, Samau Id, 0–36 metres, Siboga Stn 60, 303	Harmer, 1957		*T. celleporoides*
*Sulu Sea	6°04′30″ N, 120°59′30″ E, 42 metres, Albatross Stn D5145 and 7 other Stations, 37–420 metres	Canu & Bassler, 1929	1931.12.30.35	*T. celleporoides*
*Philippines	12°38′15″ N, 122°12′30″ E, 68 metres, Albatross Stn D5179	Canu & Bassler, 1929		*T. spathulata*
*Philippines	11°09′15″ N, 123°50′ E, 58·5 metres, Albatross Stn D5192	Canu & Bassler, 1929		*T. celleporoides*
New Guinea	1°42′30″ S, 130°47′30″ E, 32 metres, Siboga Stn 164	Harmer, 1957	1961.10.30.12, 13, 15	*T. celleporoides*
*Kei Is	4°50′ S, 131° E, Tiur Id, 0–54 metres, Siboga Stn 248	Harmer, 1957	1961.10.30.8, 9	*T. spathulata*
Kei Is	5°30′ S, 132°20′ E, 22 metres, Siboga Stn 258	Harmer, 1957	1961.10.30.14	*T. celleporoides*
*Aru Is	5°30′ S, 134°00′ E, 13 metres, Siboga Stn 273	Harmer, 1957	1961.10.30.16, 17	*T. celleporoides*
N. E. Australia	Torres Straits, 5–21 metres		1890.3.24.34 1890.4.16.5	*T. celleporoides*

Locality data		Reference	BMNH	Name
*N. E. Australia	10°30′ S, 142°30′ E, 14·6 metres, Challenger Stn 186	Busk, 1884	1887.12.9.560–562, 1944.1.8.272, 1963.2.12.281	*T. celleporoides*
*N. E. Australia	Approx. 16°23′ S, 14 miles off Queensland coast, Batt Reef, Gt Barrier Reef		1939.2.4.1	*T. spathulata*
*N. E. Australia	23°25′ S, 151°55′ E, Heron Id, Gt Barrier Reef	R. Day Coll.		*T. spathulata*



Map 1 Distribution in time and space of American, West African and European species of *Tremogasterina* (see also Appendix, p. 141). Species-groups with Recent representatives are numbered: (1) *T. subspatulata*, (2) *T. lanceolata* and the *T. mucronata*-complex, (3) *T. brancoensis*, (4) *T. oranensis*, (5) *T. perplexa* and (6) *T. musaica*.

Map 2 Distribution in time and space of East African and Indo-Pacific species of *Tremogasterina* (see also Appendix, p. 143). Species groups are numbered: (7) *T. spathulata*, (8) *T. robusta* and (9) *T. celleporoides*.

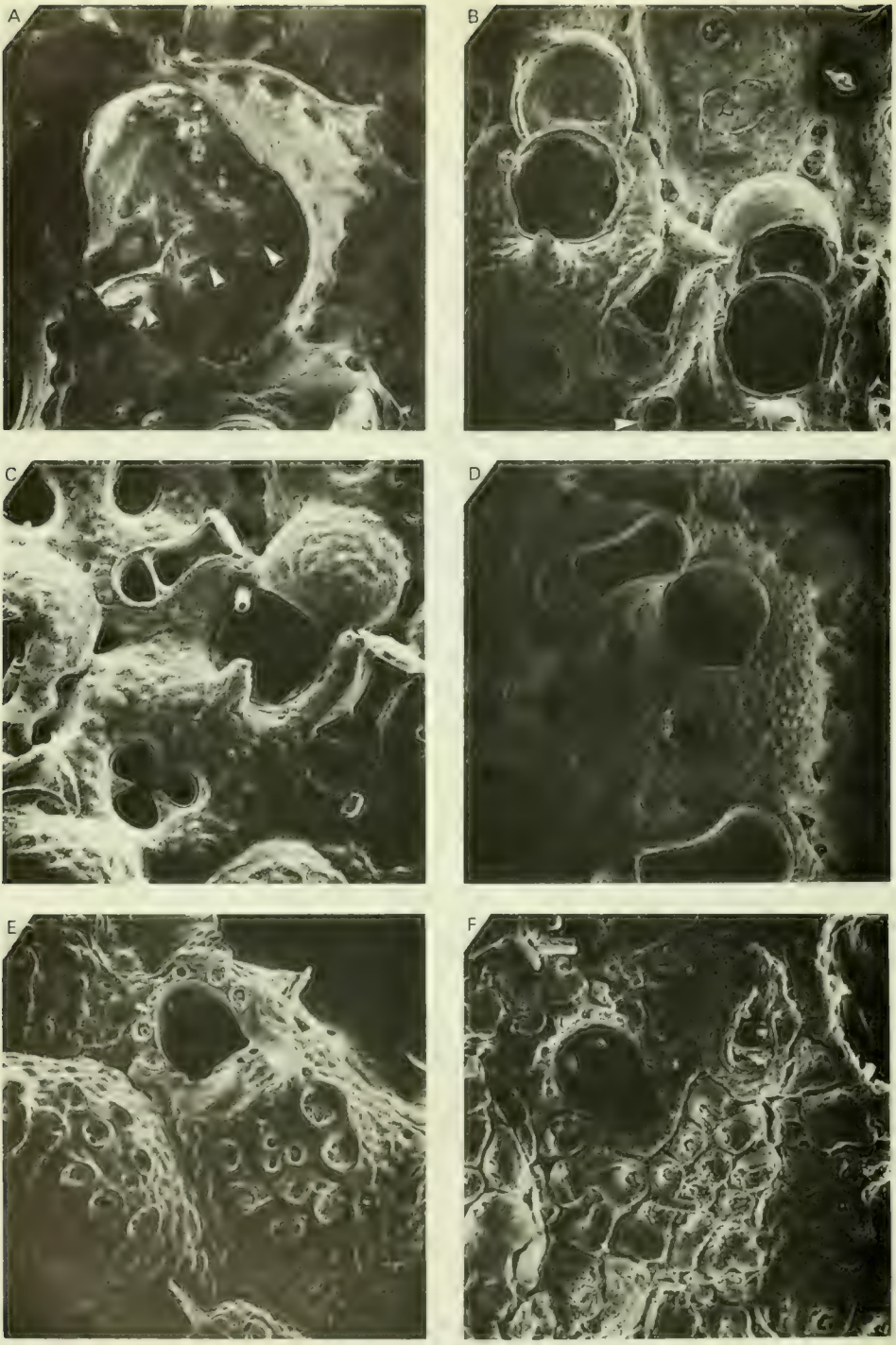

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Plate 1 *Tremogasterina* – Astogeny and ontogeny of frontal buds, ontogeny of frontal shield and brood chamber.

(A) *T. celleporoides* (Busk), Recent, Aru Is, Siboga Stn 273, BMNH, 1961.10.30.16. One of a group of frontally budded zooids. Note areolae developing around and above septulae, and pores in the 'basal' wall derived from interzooidal funnels between two zooids of the primary layer (arrowed). See also Pl. 5D. × 80.

(B) *T. mucronata* (Smitt), Recent, Kingstown Harbour, St Vincent, BMNH, 1931.5.2.6. Zooids showing late stages of ontogeny of brood chambers. Left hand brood chamber shows the two laminae fusing and is equivalent of Fig. 4F (see p. 112). Right-hand brood chamber is almost completely developed and shows secondary calcification distally (see also Plate 8C). Note spine bases and suboral mucros, and funnel incorporating three areolae (arrowed). × 72.

(C) *T. mucronata*, as above. Zooid with complete brood chamber. Note similarity of secondary thickening of brood chamber and frontal shield, the spines bases and suboral mucro and relative depression of the trifoliate foramen in the thickened frontal shield. See also Pl. 5C. × 72.

(D) *T. celleporoides*, as (A) above. Zooid showing increased depth of secondary calcified orifice with frontal thickening. Note interzooidal funnels formed from fusion and frontal extension of areolae, depressed frontal foramina and absence of spine bases. × 63.

(E) *T. perplexa* Cook, Recent, Ghana, BMNH, 1973.3.22.27. Zooid showing extension of large pits around small frontal foramina as secondary calcification increases. Note spine bases and hollow (broken) suboral mucro. See also Pl. 7E. × 94.

(F) *T. musaica* sp. nov., Recent, Ghana, BMNH, 1970.2.8.9. Zooid showing thickening of pits into blocks of calcification. Note condyles and sinuate orifice, spines bases and avicularium (at right). See also Pl. 5B. × 96.

All photographs taken using scanning electron microscope.

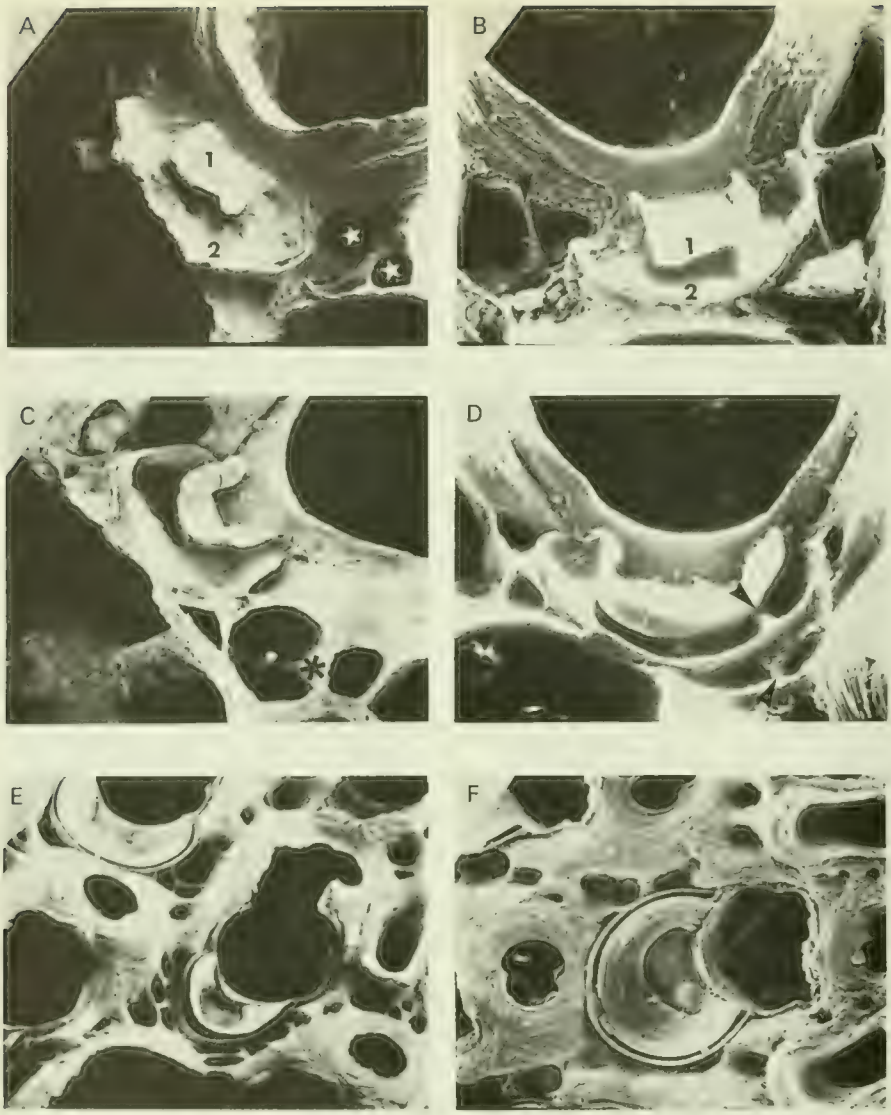
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Plate 2 Ontogeny of brood chamber in *T. celleporoides* (Busk), Recent, Torres Straits, BMNH, 1890.3.24.34. Zooids viewed from the distal–lateral side.

(A) Early stage. First lamina (1) extending distally from maternal zooid, second lamina (2) has just reached the maternal zooid wall, but has grown from the frontal shield of the distal zooid. Note that areolae of sequential zooids (*) are not yet extended and fused to form funnels. Frontal shield of distal zooid only calcified proximally, visible beneath second lamina at bottom of photograph. Equivalent of Fig. 4B. × 170.

(B) Slightly later stage. Second lamina (2) beginning to curve frontally. Note buttresses of calcification between areolae (arrowed). × 187.

(C) Later stage. First lamina (1) beginning to curve frontally. Note fusion of areolae to form a funnel (*). Frontal shield of distal zooid damaged. × 150.

(D) Slightly later stage than C. Both laminae curving frontally. Note buttresses between areolae are visible between the laminae and beneath the second lamina (arrowed). Equivalent of Fig. 4D. × 187.

(E) Later stage. Note thickening on frontal side of first lamina, and formation of funnels from areolae of the maternal and distal, and the distal and distal-lateral zooids. × 75.

(F) Later stage. Note close apposition of the laminae prior to fusion, and the distal–lateral funnels marking the opening of the tubular extension of one of the areolae beneath the second lamina. × 75.

For further stages, see Pl. 1B, C, *T. mucronata.*

All photographs taken using scanning electron microscope.

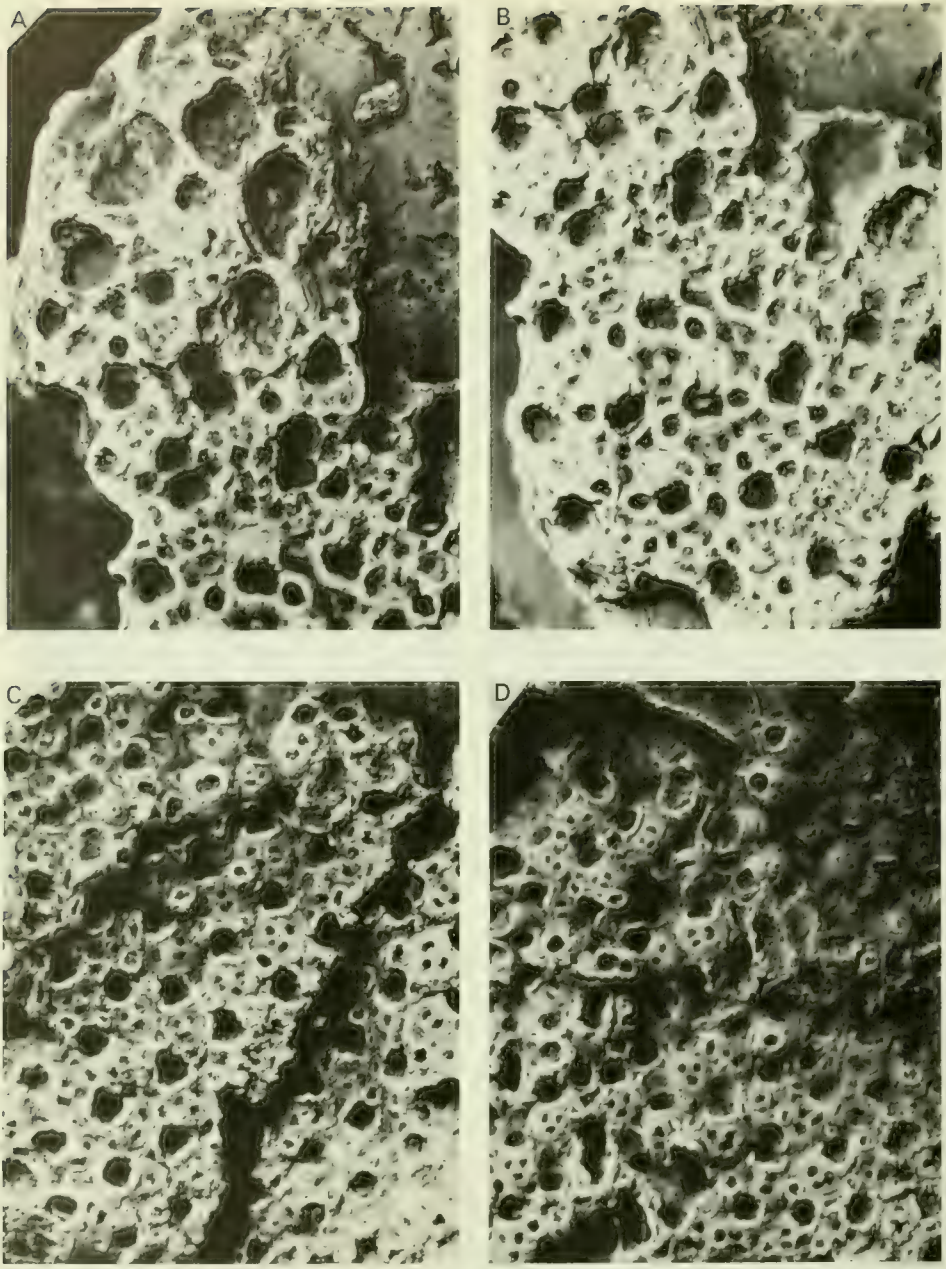
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Plate 3 Paleocene and Eocene *Tremogasterina*.

(A), (B) *T. problematica* Canu. Specimen of *Tremogasterina* from Paleocene, Roca Formation, Bertel's locality BJ-7 (see p. 127). Note small zooids, three foramina and avicularia and brood chambers. × 38.

(C), (D) *T. maçonnica* (Canu), Eocene, Tunisia. Photographs of type specimen of *Poricella maçonnica* Canu from Paris Museum. Note small zooids, prominent apertural bar, three foramina and small, randomly orientated avicularia. In (D) note numerous (broken) 'hyperstomial ovicells' (brood chambers). × 38.

All photographs taken by Dr A. H. Cheetham.

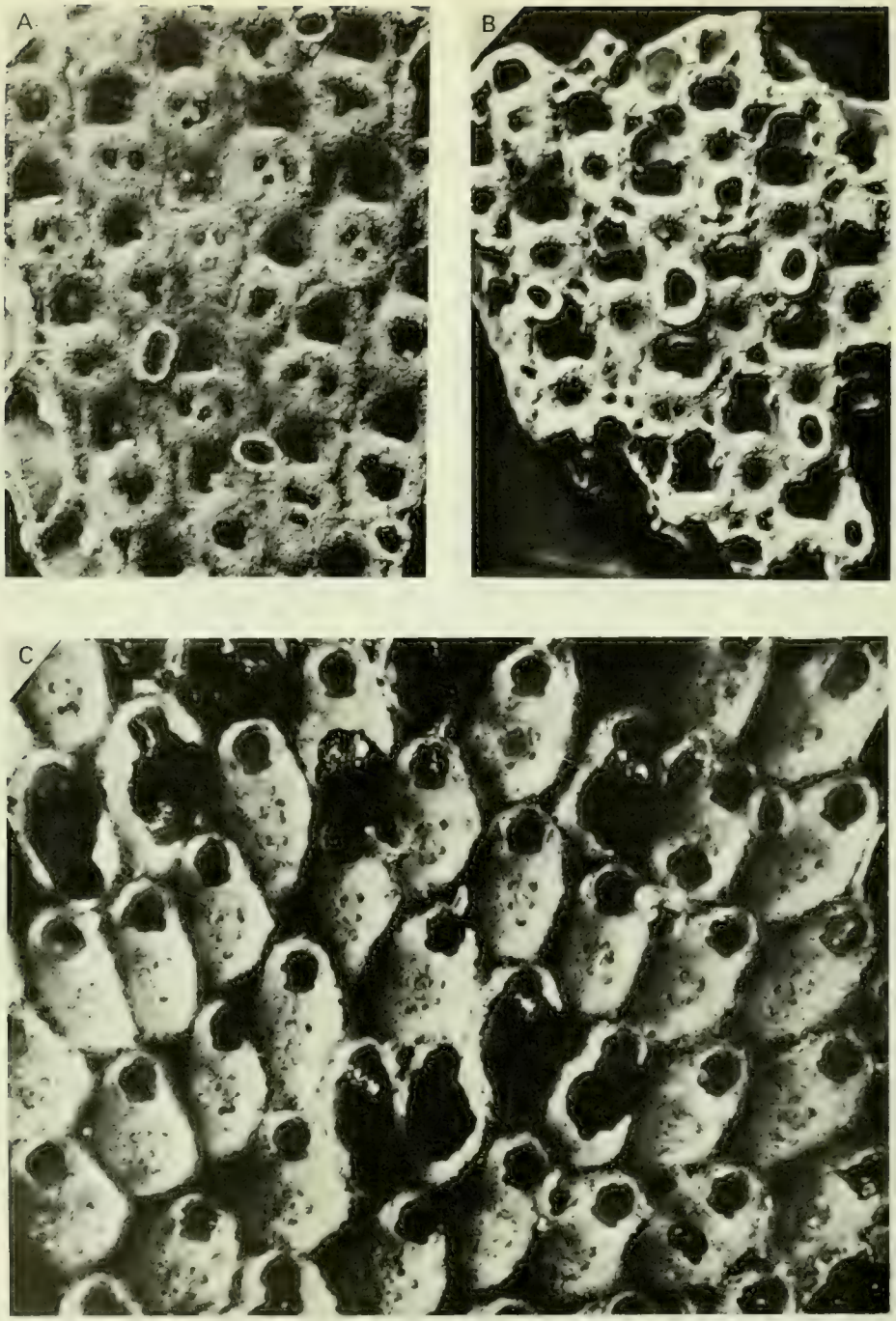
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Plate 4 Miocene *Tremogasterina*.

(A), (B) *Tremogasterina* '*miocenica*'. Specimen of *Tremogasterina* from Miocene oyster bed, Givhans Bridge, South Carolina, U.S.A. Compare Fig. 8B. Note fairly small zooids, three foramina, raised, randomly orientated avicularia and broken but prominent brood chambers. × 39. (photographs by Dr A. H. Cheetham).

(C) *Tremogasterina pouyetae* sp. nov. Part of the holotype colony, Miocene, Hèrault, France. Note excellent preservation, large zooids, elongated orifices and large number of frontal foramina. See also Fig. 6B. × 42 (photograph by P. J. Chimonides).

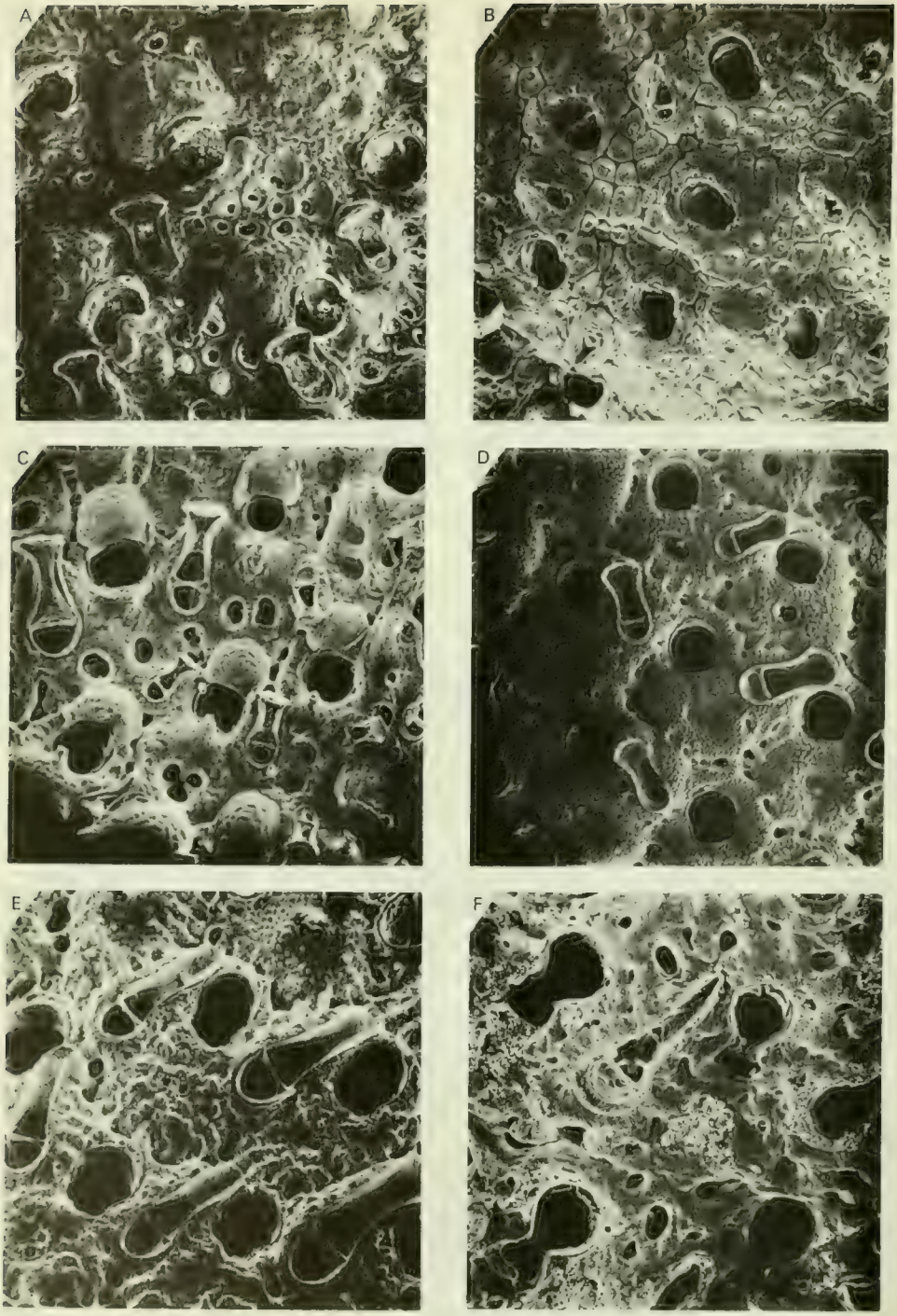
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Plate 5 Recent *Tremogasterina.*

(A) *T. spathulata* (Canu & Bassler), South China Sea, BMNH, 1962.2.20.8. Note large number of frontal foramina, with formation of surrounding funnels, spathulate, truncate avicularia and wide brood chambers. Compare Fig. 8A. × 64.

(B) *T. musaica* sp. nov., Ghana, BMNH, 1970.2.8.9. Note the blocks of calcification surrounding the frontal foramina, the sinuate orifices, the spine-bases and small, acute avicularia. See also Pl. 1F. × 60.

(C) *T. mucronata* (Smitt), Kingstown Harbour, St Vincent, BMNH, 1931.5.2.6. Note the large, trifoliate or paired foramina, the long suboral mucros, the truncate avicularia and brood chambers raised above the secondary calcified orifice. See also Pl. 1B, C. × 36.

(D) *T. celleporoides* (Busk), Aru Is, Siboga Stn 273, BMNH, 1961.10.30.16. Note the interzooidal funnels and randomly orientated avicularia. See also Pl. 1A. × 36.

(E) *T. robusta* (Hincks), Gulf of Oman, BMNH, 1972.7.1.13. Note the elongated, slightly sinuate orifices, the small frontal foramina, the spine-bases and very large, asymmetrically developed avicularia. × 60.

(F) *T. oranensis* (Waters), Senegal, BMNH, 1964.9.1.57. Note the very large condyles, the 'cleithridiate' orifice and the large, acute avicularia. See also Pl. 7C, D. × 72.

All photographs taken using scanning electron microscope.

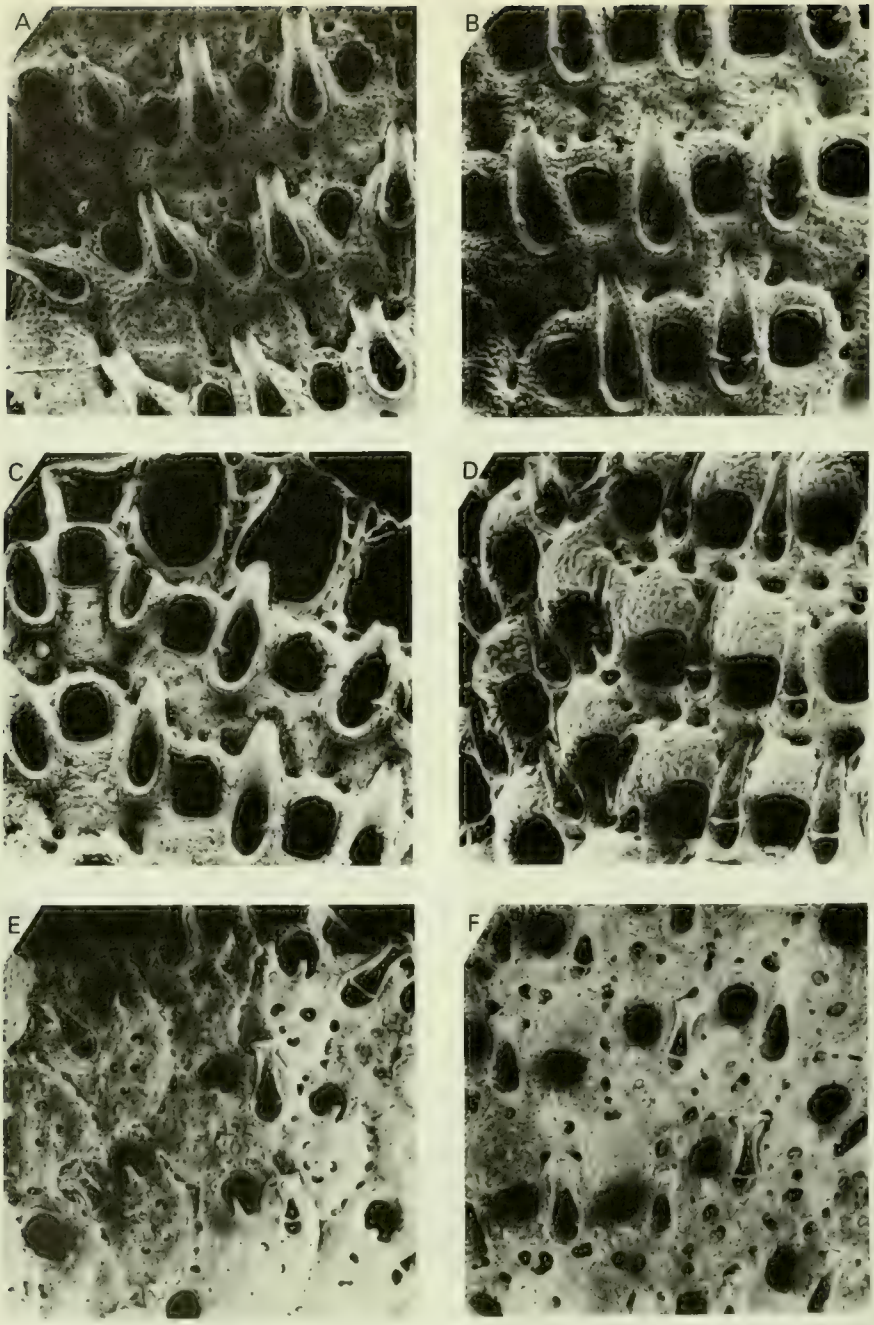
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Plate 6 Recent *Tremogasterina* from the American region.

(A) *T. lanceolata* Canu & Bassler, North of Cuba, Albatross Stn 2320, BMNH, 1932.3.7.61. Note the small, elongated orifices, the numerous but occluded frontal foramina and the large foramina caused by the development of the elongated avicularian rostra. × 43.

(B) *T. subspatulata* Osburn, part of type material of *T. subspatulata*. Clarion Id, California, USNM. Note 'verticillate' arrangement of zooids and '*lanceolata*' development of avicularia. Note spine-bases. × 39.

(C) *T. subspatulata*, as above. Growing edge, note membranimorph zooids, and rapid calcification of previously budded zooid rows, and development of secondary thickening. × 39.

(D) *T. subspatulata*, Bay of California, Albatross Stn 3005, USNM. Specimen with brood chambers, note smaller, but acute avicularia. × 42.

(E) *T. mucronata* (Smitt), Discovery Bay, Jamaica, BMNH, 1966.1.6.1. Note the truncate avicularia and very long suboral mucros. × 45.

(F) *T. mucronata*, Porto Rico, Caroline Stn 104, USNM. Note occlusion of less numerous frontal foramina. × 32.

All photographs taken using scanning electron microscope.

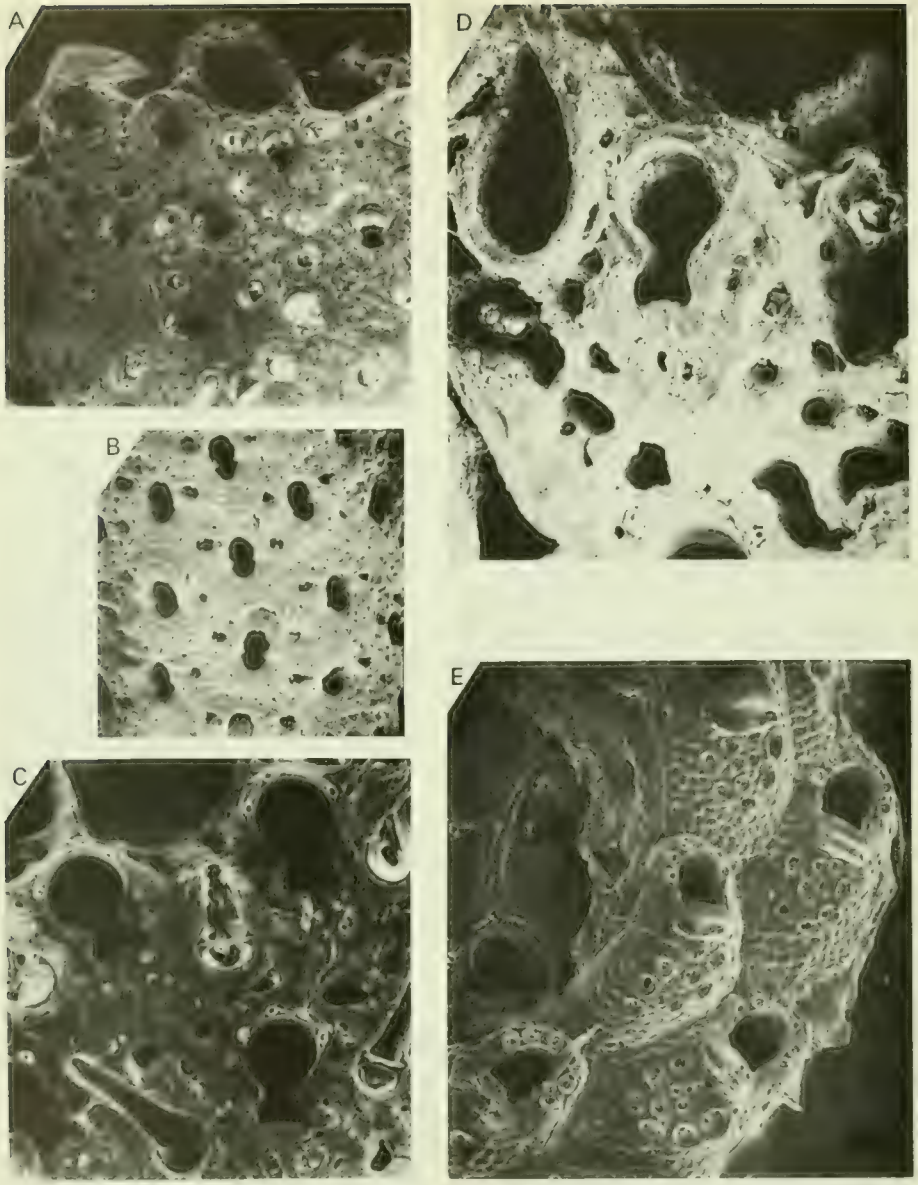
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Plate 7 Recent *Tremogasterina* from the west African region.

(A) *T. brancoensis* (Calvet), Cape Verde Is, BMNH, 1964.9.1.42. Specimen with 'typical' characters of orifice with short sinus and laterally orientated, rounded avicularia. × 39.

(B) *T. brancoensis*, Bay of Biafra, BMNH, 1964.9.1.40. Specimen with intermediate characters of orifice with deep sinus and laterally orientated, acute avicularia. × 35.

(C) *T. oranensis* (Waters), Guinea, BMNH, 1970.8.10.9A. Zooids near the growing edge. Note spine-bases and minute frontal foramina. × 85.

(D) *T. oranensis*, Senegal, BMNH, 1964.9.1.37. Zooid and avicularium at growing edge. Note very thick calcification, lateral areolae and proximal funnels and minute frontal foramina. See also Pl. 5F. × 100.

(E) *T. perplexa* Cook, Ghana, BMNH, 1973.3.22.27. Zooids growing over *Floridina antiqua*. Note funnels surrounding frontal foramina, spine-bases and suboral thickening preceding growth of mucronate process. See also Pl. 1E. × 58.

All photographs taken using scanning electron microscope.

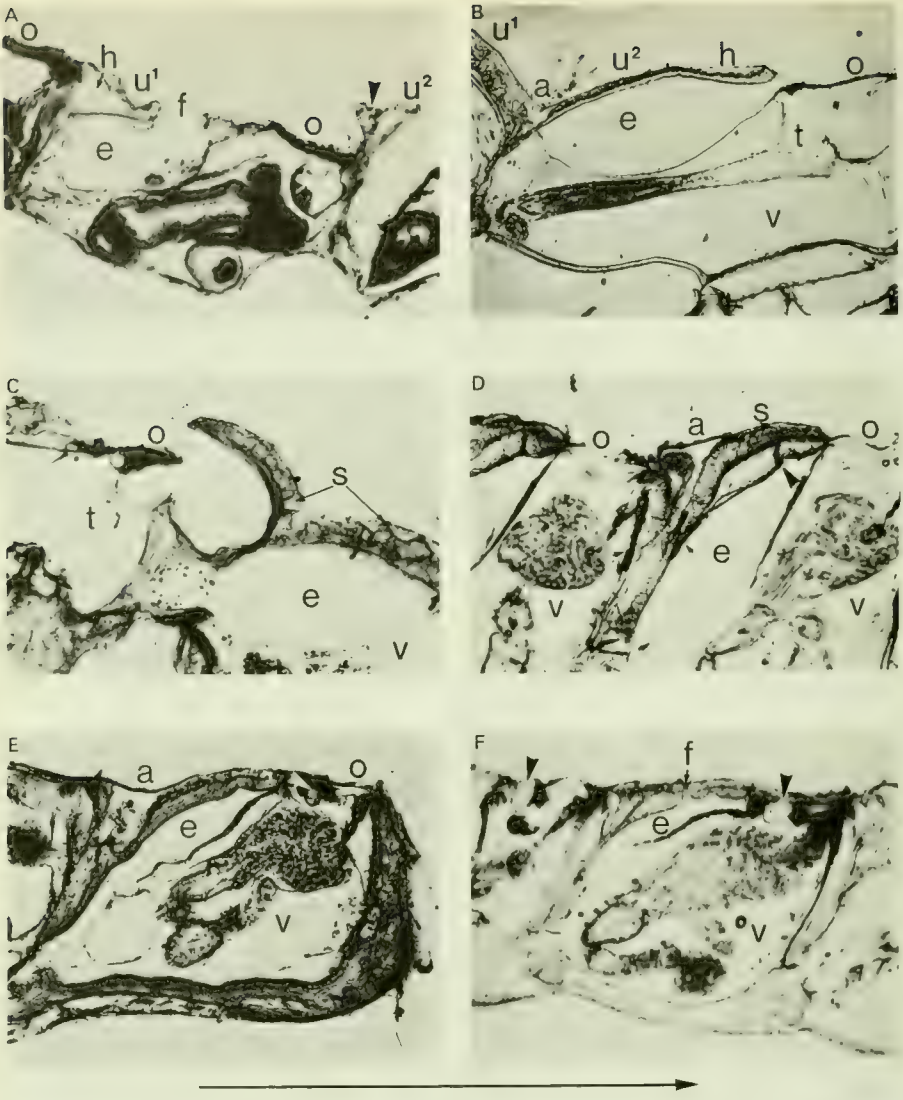
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Plate 8 Longitudinal thin-sections of zooids of Recent *Tremogasterina*.

a areola; *e* epistegal space; *f* frontal foramen; *h* hypostegal coelome; *o* operculum; *s* secondary calcification; *t* tentacle sheath; u^1 umbonuloid fold proximal zooid; u^2 umbonuloid fold distal zooid; *v* visceral coelome.

Direction of growth arrowed.

(A) *T. celleporoides* (Busk), Kei Is, Siboga Stn 258, BMNH, 1961.10.30.14. Zooid early in ontogeny. Note large frontal foramen and part of umbonuloid fold forming distal part of secondary calcified orifice (arrowed). × 63.

(B) *T. robusta* (Hincks), Gulf of Oman, BMNH, 1972.7.1.13. Zooid early in ontogeny. Note very thin calcification of frontal shield, and compare thickness in part of proximal zooid to left of photograph. × 84.

(C) *T. robusta*, as above. Brood chamber. Compare Fig. 4F. × 75.

(D) *T. brancoensis* (Calvet), Cape Verde Is, BMNH, 1964.9.1.43. Zooids later in ontogeny. Position of septulae at base of areolar tubes (small arrows). Position of frontal foramen passing through primary calcification only (large arrow). × 76.

(E) *T. oranensis* (Waters), Ghana, BMNH, 1964.9.1.35. Zooid near growing edge. Position of condyle (arrowed). × 76.

(F) *T. oranensis*, as above. Zooids later in ontogeny. Note condyles (arrowed) and frontal foramen. × 82.

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D. I. Gibson & R. A. Bray

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The Azygiidae, Hirudinellidae, Ptychogonimidae, Sclerodistomidae and Syncoeliidae (Digenea) of fishes from the northeast Atlantic

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Synopsis

Keys, descriptions (mainly original), full host-records, locality data and comments on some aspects of their biology are presented for all of the species of the hemiuroid families Azygiidae, Hirudinellidae, Ptychogonimidae, Sclerodistomidae and Syncoeliidae recorded from the northeast Atlantic region. The species described are: *Otodistomum veliporum*, *O. cestoides*, *O. plunketi*, *Otodistomum* sp. metacercariae, *Hirudinella ventricosa*, *Botulus microporus*, *Lampritrema miescheri*, *Ptychogonimus megastoma*, *Prosorchiopsis legendrei*, *Copiatestes filiferus* and, in addition, *Distoma gigas* of unknown family. The *Otodistomum veliporum–cestoides* problem is examined and discussed in detail. It is proposed that the family Hirudinellidae is composed of three monotypic genera, *Hirudinella*, *Botulus* and *Lampritrema*. *Distoma microporum* Monticelli and *Lampritrema miescheri* (Zschokke) are considered to be senior synonyms of *Botulus alepidosauri* Guiart and *Lampritrema nipponicum* Yamaguti, respectively. It is considered that the genus *Copiatestes* Crowcroft is distinct from *Syncoelium* Looss, and that *C. filiferus* (Leuckart, in Sars) belongs to this genus. It is suggested that *Distoma gigas* Nardo is a hemiuroid, possibly being related to the sclerodistomids.

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Introduction

This is the second in a projected series of papers on the helminth-fauna of fishes from the north-east Atlantic region. The families dealt with, the Azygiidae, Hirudinellidae, Ptychogonimidae, Sclerodistomidae and Syncoeliidae, with the Accacoeliidae which has already been studied (Bray & Gibson, 1977), are all members of the superfamily Hemiuroidea Looss, 1899. This group of families tends to be relatively rare or restricted to certain hosts in the marine environment. They are usually somewhat larger than, and, we believe, more primitive than, the remainder of the hemiuroid families, which we hope to deal with in a future paper. The classification and phylogenetic relationships of the Hemiuroidea will be commented upon in detail elsewhere (Gibson & Bray, in preparation).

Materials and methods

The materials and methods used in this investigation are outlined in the first paper in this series (Bray & Gibson, 1977). In addition to the sources of material mentioned in our previous report, we have now collected material at Split, Yugoslavia, in 1975 (by D. I. G.), aboard the R.V. *Cirolana* in the NE Atlantic in 1976 (by R. A. B.) and at Kristineberg Zoological Station, Sweden, in 1976 (by D. I. G.). We have used the classification of fishes presented by Greenwood *et al.* (1966) and Compagno (1973).

Terminology

Several new anatomical terms used in this paper require explaining, although detailed definitions of these terms will be presented elsewhere (Gibson & Bray, in preparation). A *prostatic sac* is the term used by Gibson (1976) to describe the muscular sac which surrounds the pars prostatica and seminal vesicle of the azygiids. A *rudimentary Juel's organ* is a distal dilation of a blind Laurer's canal which contains disintegrating seminal and vitelline material, and is probably associated with the breakdown and reabsorption of these waste products. A *rudimentary seminal receptacle* is a very small proximal dilation of Laurer's canal, where spent seminal material and excess vitelline material are stored (? and killed), before being passed down Laurer's canal. In a fully developed *Juel's organ* (Gibson & Bray, 1975), which occurs in many of the more advanced hemiuroids, the terminal bulb of Laurer's canal (rudimentary Juel's organ) actually envelops the rudimentary seminal receptacle, forming a distinct oval structure. All of the above arrangements of the proximal female reproductive system occur in the presence of a uterine seminal receptacle.

Systematic section

Family **AZYGIIDAE** Lühe, 1909

Aphanhysteridae Guiart, 1938.

DIAGNOSTIC FEATURES. Body large or small; usually elongate. Body-surface smooth, without spines or plications. Oral and ventral suckers well developed; latter in middle or anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus usually short. Gut-caeca terminate blindly close to posterior extremity. Testes two; in tandem, oblique or symmetrical; pre- or post-ovarian; in hindbody. Seminal vesicle tubular, usually short, thin-walled; convoluted in forebody. Pars prostatica tubular. Prostatic sac present surrounding pars prostatica and seminal vesicle. Ejaculatory duct usually long and convoluted, but of variable length. Hermaphroditic duct short; at distal extremity of sinus-organ. Permanent sinus-organ of variable length; usually conical. Sinus-sac absent. Genital pore mid-ventral in forebody. Ovary oval; pre- or post-testicular. Mehlis' gland pre-ovarian. Laurer's canal and uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle* absent. Uterus entirely or almost entirely pre-ovarian;

* Terminology for modifications of Laurer's canal as used by Gibson & Bray (in preparation). See above: 'Terminology'.

coiled mainly in hindbody. Eggs numerous; small; non-filamented. Vitellarium follicular; usually present laterally in much of hindbody, occasionally extending into forebody. Excretory vesicle Y-shaped, arms uniting in forebody or not. Parasitic in stomach. or occasionally body-cavity, of elasmobranchs and freshwater bony fishes.

Subfamily **AZYGIINAE** Lühe, 1909

Aphanhysterinae Guiart, 1938.
Gomtiotrematinae Gupta, 1955.
Allogomtiotrematinae Yamaguti, 1958.
Proterometrinae Yamaguti, 1958.

DIAGNOSTIC FEATURES. Body normally relatively large; occasionally small. Testes post-ovarian.

Otodistomum Stafford, 1904

Xenodistomum Stafford, 1904.
Aphanhystera Guiart, 1938.

DIAGNOSTIC FEATURES. Body large; spatulate to elongate. Ventral sucker larger than oral sucker; close to anterior extremity. Testes tandem or slightly oblique. Sinus-organ capable of considerable extension or may contract to form small papilla. Uterine field almost entirely between ovary and ventral sucker. Vitelline follicles extend in lateral fields posteriorly to ventral sucker, reaching back to post-testicular region where fields are, at least to some extent, confluent. Excretory arms usually unite in forebody, but occasionally do not. Parasitic in stomach or body-cavity of elasmobranchs (sharks, rays and chimaeras).

TYPE-SPECIES. *Otodistomum veliporum* (Creplin, 1837) (by monotypy).

The *Otodistomum veliporum–cestoides* problem

(1) *History*

Over the years there has been a great deal of confusion concerning the problem of whether there are one or two species of the genus *Otodistomum* which parasitize the stomach of elasmobranchs. *Distoma veliporum* is the name first used by Creplin in 1837 for specimens, which he later (1842) described in greater detail, from the stomach of the shark *Hexanchus griseus* in the Mediterranean Sea. Although most of the early records of this species and its synonyms were from sharks, Olsson (1868a, 1868b, 1869, 1876), Lönnberg (1889a, 1889b, 1890, 1891), Linton (1898, 1901), Jägerskiöld (1900), Stafford (1904) and Lebour (1908) all recorded it from rays. The combination *Otodistomum veliporum* was first used by Stafford (1904) when he erected this genus after examining specimens from *Raja laevis* off the eastern coast of Canada.

The name *Distoma cestoides* was first used by van Beneden (1871) for specimens from *Raja batis* off the Belgian coast. After examining specimens and studying the literature, Odhner (1911) came to the conclusion that the form from sharks, which he called *Otodistomum veliporum*, differed from the form from rays, for which he coined the combination *O. cestoides*, since van Beneden's *D. cestoides* was the oldest available name for the ray-parasite. Odhner (1911) distinguished the two species as follows:

O. veliporum [size 50 × 5–6 mm; sucker-ratio 3 : 5; anterior limit of vitellarium behind middle of uterine field and compressed into narrow lateral bands; eggs 86 × 60–63 μm; shell-thickness 6 μm; parasite of sharks.]

O. cestoides [size up to 65 × 3–5 mm; sucker-ratio 3 : 4; anterior limit of vitellarium usually in front of middle of uterine field and not so narrowly compressed into lateral bands; eggs 65–72 × 43 μm; shell-thickness 3μm; parasite of rays.]

Odhner (1911) also noted that the material collected by Lönnberg (1898) from the shark *Chlamydoselachus anguineus* off northern Norway appeared to be *O. cestoides* rather than *O. veliporum*.

This would appear to have simplified the matter a great deal. Manter (1926), however, compared in great detail material from *Raja laevis* off the eastern coast of the U.S.A., which he called *O. cestoides*, with material from *R. binoculata* off the west coast of the U.S.A., which he called *O. veliporum*. Why Manter considered the specimens from *R. binoculata* to be *O. veliporum* is not clear; but he concluded that the only significant difference between the two species was egg-size, an average of 69·4 × 46·2 μm for '*O. cestoides*' and an average of 85·5 × 57·8 μm for '*O. veliporum*'. Dollfus (1937a), in a very detailed study, considered that Manter's two 'species' were in fact two subspecies, *O. cestoides cestoides* and *O. cestoides pacificum*, and that *O. veliporum*, which he subdivided into three subspecies, occurred only in sharks and torpedoes. Van Cleave & Vaughn (1941), after examining more material from *R. binoculata* and *R. laevis*, indicated that the egg-sizes of the specimens of *Otodistomum* were not significantly different (60–94 × 40–70 μm and 55–90 × 36–58 μm, respectively), and, therefore, could not be differentiated even at the sub-specific level. These authors concluded that the American form of *Otodistomum* comprised a single variable species to which the name *O. cestoides* could be applied. Later workers, led by Dawes (1946) who based his conclusions mainly upon Manter's initial assumption that he was in fact dealing with specimens of *O. veliporum*, have considered *O. cestoides* and *O. veliporum* to be synonymous. Dawes concluded his contribution thus: 'Pending further inquiries, which will not provide a very attractive problem, it seems logical to conclude that a single species of the genus *Otodistomum* infects cartilaginous fishes all over the world, and that it should be known not as *O. cestoides* but as *O. veliporum*.' It was not until the work of Kay (1947) that a North American worker examined specimens of *Otodistomum* from a shark, and on this occasion it was described as a new species, *O. plicatum*. As pointed out by Gibson (1976) this species is not only morphologically very similar to *O. veliporum* (in the European sense), but was also recorded from the type-host, *Hexanchus griseus*, of the latter species, and thus can probably be regarded as a synonym. Recently, Brinkmann (1975) has followed Dawes (1946) in considering that there is a single worldwide species of *Otodistomum*, but indicates that morphological differences observed in different hosts and in different geographical regions may possibly warrant the recognition of subspecies. He also suggests that larger specimens may produce larger eggs than do the smaller ones and that larger elasmobranchs may entertain larger specimens of '*O. veliporum*'. Finally, Gibson (1976), after studying specimens in the collection of the British Museum (Natural History) from sharks and rays, recognized both *O. veliporum* and *O. cestoides* as valid species. He stated that while variations of 20 μm were found in the length of eggs from the same worm and 40 μm in eggs from the same host-species, the specimens from rays (*O. cestoides*) had an egg-length usually within the limits 60–90 μm and a shell-thickness of 3–6 μm, and specimens from sharks (*O. veliporum*) had an egg-length usually within the limits 80–120 μm and a shell-thickness of 5–8 μm. Gibson also noted that there was a relationship between the size of the worm and the egg-size and suggested that this might be the result of growth in the oötype. He agreed with Odhner's (1911) comments about the anterior limit of the vitellarium in the two species, and implied that he considered the specimens which he examined from the shark *Centroscyllium fabricii* to be *O. cestoides* rather than *O. veliporum*.

There are, therefore, two schools of thought: one which considers that there is a single species of *Otodistomum* which occurs in the stomach of elasmobranchs and the other which considers that there are two species, *O. veliporum*, occurring in sharks and torpedoes, and *O. cestoides*, occurring mainly in rays but on rare occasions in sharks.

(2) *Criteria*

In an attempt to resolve this problem we decided to investigate the various criteria which have been used by authors, especially Odhner (1911), for distinguishing the two species. With this aim in mind, we examined a great deal of material from the collection of the British Museum (Natural History) in addition to that which we have collected ourselves. This material represents a much wider variety of hosts and larger number of specimens than appears to have been studied by other authors.

Firstly, dealing with the criteria listed by Odhner (1911):

(a) Maximum length

Table 1 shows the maximum length of specimens of *Otodistomum* from the stomach of various species of host. We have included data from the literature in this table to give a more comprehensive range.

Table 1 The maximum length (mm) of specimens of *Otodistomum* recorded from different hosts.

Host	Present work	From the literature
Hexanchus griseus	–	101 (Dollfus, 1937a)
Dalatias licha	92	135 (Bråten, 1964)
Echinorhinus brucus	–	52 (Guiart, 1938)
Centroscymnus coelolepis	35	38 (Guiart, 1938)
Centroscyllium fabricii	31	–
Sharks	–	55 (Mühlschlag, 1914)
Sharks	–	50 (Odhner, 1911)
Torpedo spp.	–	51.8 (Tendeiro & Valdez, 1955)
Raja batis	46	(*c.* 37) (van Beneden, 1871, figure)
Raja binoculata	–	69 (van Cleave & Vaughn, 1941)
Raja jenseni	48	–
Raja laevis	–	65 (Manter, 1926)
Raja nidarosiensis	62	–
Raja radiata	23	52 (Layman & Borovkova, 1926)
Raja richardsoni	75	–
Raja spinicauda	33	–
Raja sp. (? *griseocaudata*)	–	20 (Gibson, 1976)
Raja spp.	–	65 (Odhner, 1911)

These results illustrate the wide variation in size attained in different species of host; but tell us little except that the specimens from *Dalatias licha* and *Hexanchus griseus* appear to be capable of reaching a much greater length than specimens from the remainder of the hosts. A great variation in size was noticeable in material we examined from various species of ray. Although we did not find any specimens from *Raja radiata* or *Raja* sp. (? *griseocaudata*) which reached more than 23 mm in length, both Lebour (1908) and Layman & Borovkova (1926) have reported much larger specimens from the former species. This illustrates the danger of relying upon material from a small number of host-specimens caught at the same time of the year, as we have no data on any relationship between season and size of the parasites. There is evidence that the average and maximum size of these parasites is different in various species of ray, but final proof that this is a host-induced effect must await the results of carefully controlled experiments involving the feeding of uninfested rays of various species with metacercariae from the same species of teleost. In connection with this, it is worthy of note that *Otodistomum* is quite unknown in certain common species of ray, e.g. *R. naevus*.

(b) Sucker-ratio

Sucker-ratio is generally considered to be a relatively good specific criterion. Although there are indications in some groups that allometric growth may occur, our observations and the comprehensive series of measurements of Manter (1926, table 4) indicate that the sucker-ratio is relatively constant, irrespective of the size of the specimen. Our results (Table 2) show that, except for the specimens from *Dalatias licha*, the sucker-ratio of the specimens are very similar, regardless of host. The specimens from *D. licha*, although there might be a slight overlap in extreme cases, almost always have a significantly smaller oral sucker relative to the ventral sucker. This strongly suggests that more than one species is involved. Care should be taken, however, in assessing ratios taken from flattened specimens, as the pressure needed to flatten these large worms cause the more protruded ventral sucker to increase in size relative to the oral sucker. Such specimens have not been included in our results.

(c) Distribution of vitelline follicles

(i) Anterior limit. The results of this investigation (Table 2) indicate that the anterior limit of the vitelline follicles is a very variable feature, in the majority of cases reaching anteriorly to the middle of the uterine field. Admittedly, in the specimens from *Dalatias licha* the follicles tend not to reach quite as far forward as in the specimens from the other hosts; but it does not appear that this is significant. These results, therefore, suggest that, although in specimens from some hosts the follicles tend to reach well anteriorly to the middle of the uterine field, this feature is far too variable and the differences too small for this to be a reliable criterion. There is also some evidence that the follicles reach further anteriorly in small specimens: this would account for the high percentage given for specimens from *R. radiata* and *R.* sp. (? *griseocaudata*), the latter being 70–80%.

Table 2 The sucker-ratio and anterior limit of the vitellarium of specimens of *Otodistomum* from various hosts.

	Sucker-ratio		Anterior limit of vitellarium	
Host	Range	Mean	Range	Mean
Dalatias licha	1·5–2·1	1·8	33–60	50
Centroscymnus coelolepis	1·25–1·5	1·4	60–78	68
Centroscyllium fabricii	1·3–1·6	1·45	44–77	65
Raja batis	1·25–1·55	1·4	42–73	55
Raja jenseni	1·3–1·4	1·35	55–70	62
Raja radiata	1·2–1·6	1·4	59–80	72
Raja richardsoni	1·25–1·6	1·4	40–68	55
Raja spinicauda	1·3–1·5	1·4	56–85	70

The sucker-ratio is represented as the width of the ventral sucker when the width of the oral sucker equals 1. The anterior limit of the vitellarium, when measured from the ovary, is represented as a percentage of the uterine field (the distance between the ovary and the ventral sucker).

(ii) Posterior limit. One feature which was very noticeable was that in specimens from *Dalatias licha* the posterior limit of the vitellarium normally extended only a short distance into the posterior half of the worm and did not extend into the posterior third. In contrast, in the specimens from other hosts the posterior limit of the vitellarium normally occurred within the posterior third of the body. Within these limits this feature is very variable, in the specimens from rays, for example, the posterior limit of the follicles ranges from just within the posterior third of the body almost to the posterior extremity. There is evidence that the follicles tend to reach further posteriorly in the smaller specimens.

(iii) The degree of lateral banding of the vitelline follicles. Odhner (1911) noted that in the specimens from sharks the follicles, presumably in the post-testicular region, tended to occur in lateral bands which were more distinct than those in the forms from rays. This banding can be clearly seen in our specimens from *Dalatias licha*; but as it also occurs in some specimens from *Raja batis* and *R. richardsoni*, we do not consider it to be a reliable feature.

(d) Egg-length

Egg-length is generally regarded as being a good specific criterion. A great deal of care must be taken when measuring eggs, as they rarely lie absolutely horizontal *in situ*. In the majority of cases in this work eggs were removed from the anterior extremity of the uterus and measured in isolation. It is important that eggs from the distal region of the uterus are examined, as those from the proximal region often have thin shells and are very susceptible to changes in shape and size caused by differences in the osmolarity of the reagents with which the worm has been treated. Even so variations of up to 20 μm were obtained for eggs from a single worm and up to 40 μm in specimens from the same host-species. This is a much greater variation than normally occurs in digeneans, but similarly large variation also occurs in other azygiids.

Results based on 40–120 eggs from each host-species (8 per worm) are presented in Table 3. These indicate that the specimens from *D. licha* have a mean egg-length which is distinctly greater

Table 3 The length and shell-thickness of eggs occurring in the distal uterus of specimens of *Otodistomum* from various hosts.

Host	Egg-length (μm)		Shell-thickness (μm)	
	Range	Mean and standard deviation	Range	Usual thickness
Dalatias licha	80–120	101 ± 7·5	4–10	6–8
Centroscymnus coelolepis	72–97	83 ± 7·5	3–4	3–4
Centroscyllium fabricii	74–102	87 ± 6	3–6·5	3–5
Raja batis	67–87	76·5 ± 5	3–7	3–4
Raja jenseni	58–94	78 ± 8	3–6	3–4
Raja radiata	59–95	72·5 ± 5	2·5–5	3–4
Raja richardsoni	68–100	83·5 ± 7·5	3·5–5	*c.* 4
Raja spinicauda	72–100	85·5 ± 7	3–6	3–5

than those from other host-species. This is not a function of the larger size of the worms, for, as illustrated in Fig. 1, although there is an initial relationship between the size of the worm and the size of the eggs in smaller specimens, after the worm reaches a certain size (about 25–30 mm) the mean egg-length tends to be relatively constant irrespective of the size of the worm. The relationship between egg-length and worm-length in the smaller specimens probably explains the apparently significant differences in the mean egg-lengths given in Table 3, particularly those from *Raja radiata* and *Centroscyllium fabricii*. Layman & Borovkova (1926), who record much larger specimens from *R. radiata*, give the egg-length as 82–98·5 μm (see Table 8). Although the standard deviation of the mean egg-length in the specimens from *D. licha* does not overlap those from the other host, the fact that their overall ranges do overlap reduces the value of this criterion. If eggs from several specimens can be measured then the mean egg-length may be a useful feature. In addition it should be noted that eggs of more than 100 μm were rarely found except in specimens from *D. licha*.

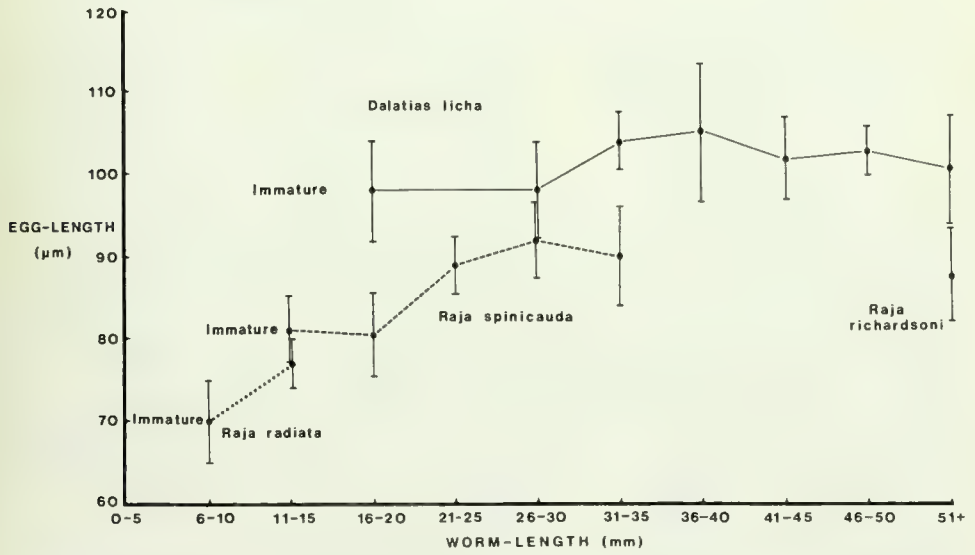

Fig. 1 Mean egg-length and standard deviation vs length of worm in different hosts.

(e) Egg-shell thickness

This feature is used by several authors to distinguish *O. veliporum* and *O. cestoides*. Egg-shell thickness is undoubtedly related to egg-size, larger eggs tending to have thicker shells. Nevertheless, the results presented in Table 3 show that, although the ranges do overlap, the specimens from *D. licha* tend to have distinctly thicker shells than those from other hosts, this difference being somewhat greater than would be expected if it was related to egg-size only. Eggs from specimens from the other hosts have a relatively constant thickness. Although this feature does appear to be useful, it should not be used in isolation.

In addition to the above features, we have noticed the following differences:

(i) Pre-oral lobe. In specimens from rays the well-developed pre-oral lobe can be seen to be filled with gland-cells, when viewed in sections. They can also be seen in some whole-mount preparations. In the single sectioned specimen from *D. licha* this concentration is not present, nor does it appear to occur in the whole-mounts. We also sectioned a specimen from *Centroscymnus coelolepis*, where the gland-cells were present, but in not nearly the same concentration as in the material from rays. We feel that this observation is worth noting, although further material from other hosts must be examined before this feature can be given any credence.

(ii) The extent of the uterine field. Superficial examination of the material and figures from the literature suggests that the uterus in specimens from rays is much larger and takes up a greater proportion of the total body-length than that of the specimens from sharks. We have therefore measured our specimens and calculated the length of the uterine field, i.e. the distance between the ovary and the ventral sucker, as a percentage of the total body-length.

Table 4 presents the results from mature specimens only (i.e. those containing eggs), as the uterine field of immature specimens is noticeably shorter. This latter feature is illustrated by Fig. 2,

Table 4 The length of the uterine field (the distance between the ovary and the ventral sucker) as a percentage of the total length of mature specimens of *Otodistomum* from various hosts.

Host	Range	Mean and standard deviation
Dalatias licha	11–15	13·5 ± 1·5
Centroscymnus coelolepis	17–21	19·5 ± 1·5
Centroscyllium fabricii	18–40	28 ± 7·5
Raja batis	17–28	23 ± 5
Raja jenseni	12·5–37	23·5 ± 6·5
Raja radiata	18–36	26 ± 7
Raja richardsoni	19–37	26 ± 5
Raja spinicauda	16–33	23 ± 4·5

which we have prepared from the measurements given by Manter (1926). It shows that in immature specimens the ratio of uterine field to body-length increases with body-length, but that in mature specimens the ratio is nearly constant.

Our results indicate that the uterine field : body-length ratio in mature specimens from *D. licha* is significantly smaller than those from the rest of the hosts. As the uterine field in mature specimens does not appear to show any allometric relationship to body-length, this criterion may be a sound one. Taking into account the literature and other material which we have examined, it would appear that these differences may not be so distinct (see Tables 7 and 9). Nevertheless, mature specimens resembling those from *D. licha* in other morphological features appear to have a uterine field which is less than 20% and usually less than 16%, whereas specimens from rays and some small sharks which are morphologically similar to those from *R. batis* have a uterine field which is almost always greater than 16% and usually greater than 20%.

(iii) The level of the bifurcation of the excretory vesicle. This feature, although not visible in many whole-mounts, may be of some assistance in distinguishing the two species. In specimens

from *D. licha* it usually occurs within the posterior half of the post-testicular region of the vitelline field (or even entirely posterior to the vitelline field). In the material from rays and both *Centroscyllium fabricii* and *Centroscymnus coelolepis* it normally occurs in the anterior half of the post-testicular region of the vitelline field. This feature is not absolutely constant, however, as it depends to a great extent upon the distribution of the vitelline follicles, which is in itself a variable feature. As it was visible in only a small proportion of the material, its value as a specific criterion requires further study.

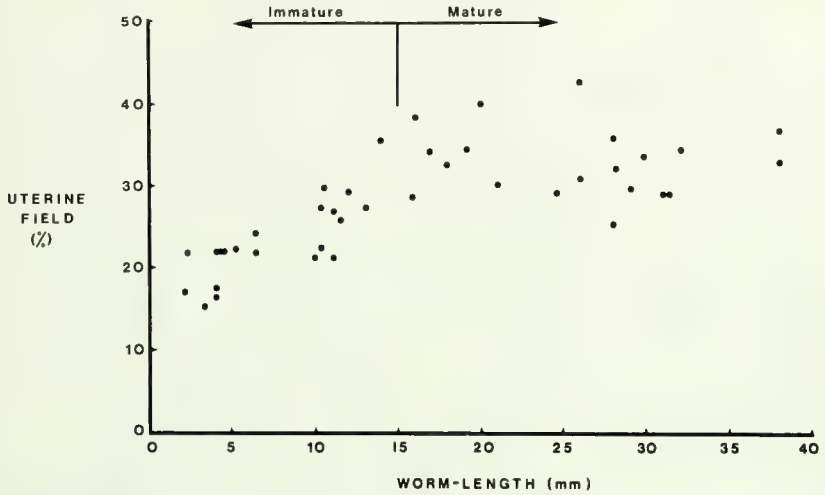

Fig. 2 Uterine field (measured from ventral sucker to posterior testis) as a percentage of body-length vs length of specimens from *Raja laevis*. These figures are calculated from measurements given by Manter (1926), and can be directly related to our measurements of the uterine field if reduced by 5% to allow for the distance between the ovary and the posterior testis.

Table 5 A summary of the features which can be used to distinguish *Otodistomum veliporum* and *O. cestoides*.

Feature	*O. veliporum*	*O. cestoides*
Length (mm)	<135	<80
Sucker-ratio (breadth)	Normally 1 : 1·5–2·1	Normally 1 : 1·2–1·6
Anterior limit of vitellarium	1/3 to 2/3 of distance from ovary to ventral sucker	2/5 to 4/5 of distance from ovary to ventral sucker
Posterior limit of vitellarium	Does not normally extend into posterior third of body*	Normally extends into posterior third of body
Uterine field (in mature specimens)	Normally less than 1/6 of body-length	Normally more than 1/6 of body-length
Level of excretory bifurcation	Usually posterior to middle of post-testicular region of vitelline field	Usually anterior to middle of post-testicular region of vitelline field
Egg-length (μm)	80–130 (usually 90–115)	55–102 (usually 65–95)
Egg-shell thickness (μm)	4–10 (usually 6–8)	2·5–7 (usually 3–5)
Host	Hexanchiform, squaliform and squatiniform sharks and torpedoes	Rays and some small squaliform sharks

* The figure of a specimen from *Squatina californica* given by Caballero & Caballero (1969) shows the vitelline field just extending into the posterior third of the body and the uterine field reaches almost one-fifth of the body-length.

(3) *Conclusion*

The results presented above indicate quite clearly that there are two forms of *Otodistomum* present in the gut of the hosts examined, one from *Dalatias licha* and the other from the remainder. The form from *D. licha* is almost certainly *O. veliporum* (Creplin, 1837) as it appears to be morphologically identical with material described by other workers from *Hexanchus griseus*, the type-host of this species. The other form appears to be *O. cestoides* (van Beneden, 1871) which has been described by several authors, usually from rays. Another important point that this work has illustrated is that none of the features used for distinguishing these two species can be applied in isolation. At least three and preferably four or five of these criteria, which are summarized in Table 5, should be used.

We have not attempted to answer the question as to whether there are various subspecies present, as suggested by Dollfus (1937a), for, although there certainly are differences in size and morphology in specimens from different host-species, we do not know whether they are caused by environmental or genetic factors. Only with experimental work can one hope to solve this problem.

Key to the species of *Otodistomum* recorded from the northeast Atlantic

1 Parasitic in body-cavity of squaliform sharks and rays; breadth at least 1/3 of total length; uterine field normally at least 1/3 of body-length; eggs normally 100–120 μm with a shell-thickness of 6–9 μm . . . . . ***O. plunketi*** Fyfe, 1953 (p. 192)

– Parasitic in gut, especially stomach of elasmobranchs; breadth normally much less than 1/3 total length in mature specimens 2

2 Parasitic in hexanchiform, squaliform and squatiniform sharks and torpedoes; sucker-breadth ratio normally 1 : 1·5–2·1; vitellarium does not usually extend into posterior third of body; uterine field rarely more than 1/6 of total length in mature specimens; eggs 80–130 (usually 90–115) μm with a shell-thickness of 4–10 (usually 6–7) μm . . . . . ***O. veliporum*** (Creplin, 1837) (p. 176)

– Parasitic in rays and some small squaliform sharks; sucker-breadth ratio normally 1 : 1·2–1·6; vitellarium does not usually extend into posterior third of body; uterine field rarely less than 1/6 of total length in mature specimens; eggs 55–102 (usually 65–95) μm with a shell-thickness of 2·5–7 (usually 3 5) μm . . . ***O. cestoides*** (van Beneden, 1871) (p. 181)

Otodistomum veliporum (Creplin, 1837) Stafford, 1904

(?) *Distoma scimna** Risso, 1826.
Distoma scymna or *scymni* Risso of various authors.
Otodistoma scymni (Risso) Guiart, 1938, in part.
Distoma veliporum Creplin, 1837.
Otodistomum veliporum leptotheca Dollfus, 1937.
Otodistomum veliporum pachytheca Dollfus, 1937.
Fasciola squali grisei Diesing, 1850 (attributed to, but not used by, Risso, 1810).
Distomum insigne Diesing, 1850.
Distoma microcephalum Baird, 1853.
Otodistomum plicatum Kay, 1947.

TYPE-HOST AND LOCALITY. *Hexanchus griseus*, Sicily.

RECORDS.

(i) Material studied

(a) From the NE Atlantic

Dalatias licha [stomach] SW of Barra Head, Scotland (March, 1954). Collected by E. W. Whitehead. BM(NH) Reg. No. 1954.9.13.59–79.

Dalatias licha [spiral intestine] Bay of Biscay (47°N, 06°W; depth 650 m; Jan., 1971). BM(NH) Reg. No. 1973.5.17.39–41 (see Bray, 1973 : 167).

* It is possible that *Distoma scimna* of Risso (1826) is the senior synonym of *Otodistomum veliporum*; but, as Risso's description is very brief, we cannot be absolutely certain. In view of this, and after 130 years of common usage, it would seem inadvisable to replace the familiar appellation.

Dalatias licha [stomach] Off western Scotland (55°N, 10°W; depth 800–825 m; June, 1974). BM(NH) Reg. No. 1976.5.12.1–2.

Squalus acanthias [stomach] Falmouth Harbour, Cornwall, England. BM(NH) Reg. No. 49.12.29. 2–3. (Type specimens of *Distoma microcephalum* Baird, 1853.)

(b) From elsewhere

'Serrated Acanthias' [?] (?) Eastern coast of U.S.A. Collected by Dr Chapman. BM(NH) Reg. No. 1914.1.26.1–3.

(ii) NE Atlantic records from the literature

Dalatias licha [stomach] Biarritz, France (May, 1937). Dollfus (1937a : 450; 1937b : 72).

Dalatias licha [stomach] Oslo Fjord, Norway (Oct., 1962). Bråten (1964 : 73).

Dalatias licha [stomach] Shetland Is, Scotland (1953). Rae, in Bråten (1964 : 73).

Dalatias licha [spiral intestine] Northern Bay of Biscay (47°N, 06°W; depth 650 m; Jan., 1971). Bray (1973 : 167).

Echinorhinus brucus [stomach] Roscoff, Finistere, France. Villot (1875 : 477, as *Distoma scimna*; 1878 : 3, as *Distomum insigne*; redescribed by Dollfus, 1937a : 434).

Echinorhinus brucus [stomach] SW of Finistere (47°N, 05°W; depth 446 m; Sept., 1903). Guiart (1938 : 21, as *Otodistoma scymni*).

Hexanchus griseus [branchial region] Arcachon, France (March, 1902). Cuénot (1927 : 247; described by Dollfus, 1937a : 440).

Hexanchus griseus [stomach] French Atlantic Coast (47°N; April, 1934). Dollfus (1937a : 440).

Somniosus microcephalus [?] Origin unknown, but much of this shark's distribution is in NE Atlantic region. Mühlschlag (1914 : 199).

Squalus acanthias [stomach] Falmouth Harbour, Cornwall, England. Baird (1853a : 58; as *Distoma microcephalum*).

Torpedo marmorata [stomach] St Jean-de-Luz, Bay of Biscay, France (July, 1914). Dollfus (1937a : 441; 1937c : 167).

Torpedo torpedo [stomach] Coast of Algarve, Portugal (July, 1954). Tendeiro & Valdez (1955 : 95).

Host (?) [?] Vestmannaeyjar, Iceland (Aug., 1932). Brinkmann (1956 : 15).

Aspects of biology. Nothing appears to be known about the early stages in the life-history of this species, although much is known about some of the related azygiids in freshwater. In the latter cases prosobranch molluscs apparently become infested by eating embryonated eggs. The miracidia hatch within the molluscs and develop into sporocysts. These give rise to rediae, from which very large furcocystocerous cercariae are released. Upon release the body-wall of the cercaria absorbs water and expands greatly, leaving an immature adult within the anterior tail-region. The parasite enters its definitive host when the large, often colourful, cercaria is swallowed by a fish. Although it is possible that some of the fishes act as paratenic hosts, there appears to be no evidence that a crustacean host is involved. Detail of the life-histories of some these of freshwater azygiids are summarized by Yamaguti (1975).

As shown below (p. 196) metacercariae of *Otodistomum* have been found encysted, usually in the gut-wall, of teleosts, chimaeras, a ray and carcharhiniform sharks. As all the species of sharks and torpedoes infested with *O. veliporum* are piscivorous, it seems reasonable to suppose that they acquire this parasite by feeding on other fishes. These fishes, which in this instance may act as obligatory intermediate hosts, presumably acquire the parasite, if the freshwater azygiid life-history pattern can be used as a guide, by feeding directly on the cercariae, possibly by feeding on infected molluscs or by feeding on smaller infested teleosts. Most of the definitive hosts of *O. veliporum* are pelagic, but *Squatina* and *Torpedo* spp. are bottom-living, and although these fishes do feed upon small teleosts, they also feed upon molluscs; there is a possibility, therefore, that these fishes could acquire the parasites directly.

Previous descriptions. Villot (1878 : 3; as *D. insigne*); Poirier (1885 : 479; as *D. insigne*); Odhner (1911 : 516); Mühlschlag (1914 : 201); Dollfus (1937a : 433); Kay (1947 : 79; as *O. plicatum*); Tendeiro & Valdez (1955 : 95); Caballero y C. & Caballero R. (1969 : 958).

Description (Figs 3 & 4). This description is based on whole-mounts and sections of material mainly from the stomach of *Dalatias licha*. The size of these large worms is very variable, reaching

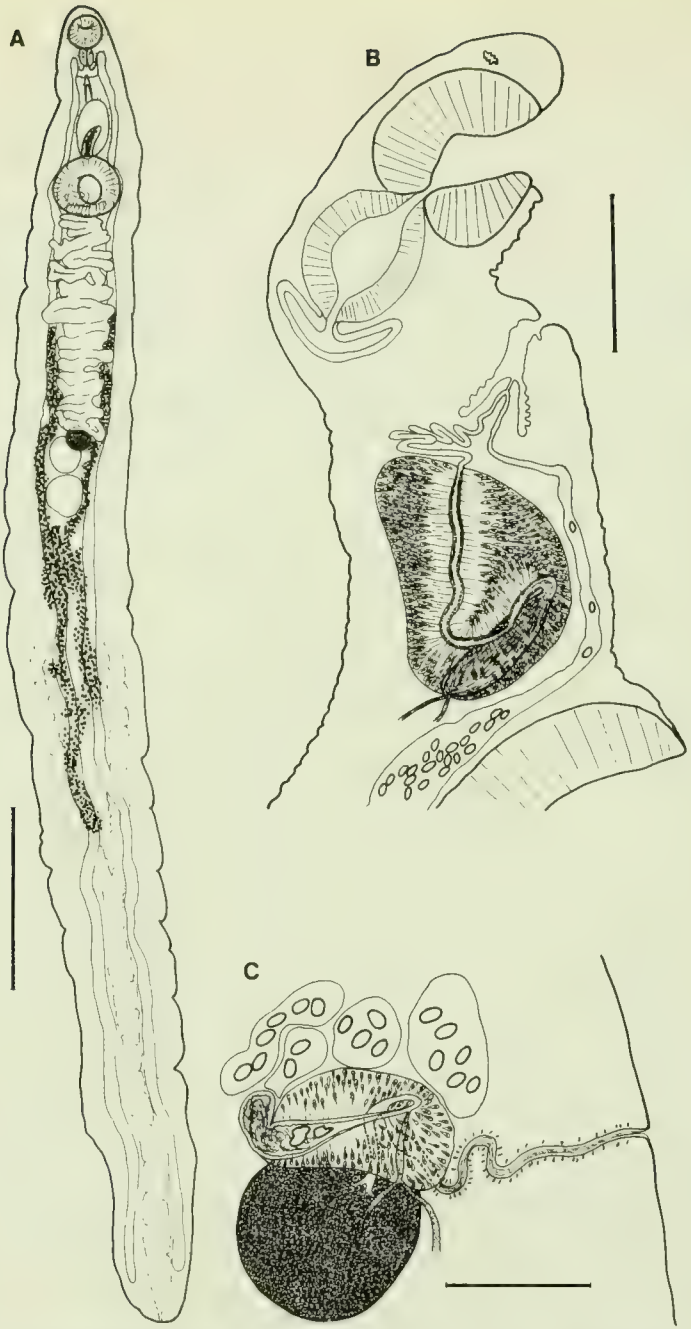

Fig. 3 *Otodistomum veliporum* ex *Dalatias licha*: (A) whole-mount; (B) sagittal section of forebody showing terminal genitalia; (C) lateral view of ovarian complex. Scale: (A) 5 mm; (B) 1 mm; (C) 500 μm.

up to 135 mm in length and 11 mm in breadth. The dimensions of the worms described are given in Table 6 and some measurements from the literature are given in Table 7. The worms are

Table 6 Measurements of *Otodistomum veliporum* from the material and hosts examined.

	Host		
	Dalatias licha	'Serrated Acanthias'	*Squalus acanthias*
Number of specimens	10	1	2
Length (mm)	13–92	40	10–14
Breadth (mm)	3–6	6	2·9–3·0
Forebody (mm)	1·7–7·5	7	–
Oral sucker (mm)	0·7–2·0 × 0·75–1·8	breadth 2·0	0·95 × 0·8–0·95
Ventral sucker (mm)	1·25–2·5 × 1·3–3·2	breadth 3·4	1·3 × 1·45
Sucker-ratio	1 : 1·5–2·1	1 : 1·7	1 : 1·5–1·8
Pharynx (mm)	0·5–1·0 × 0·4–0·7	–	–
Prostatic sac (mm)	1·1–2·0 × 0·75–1·3	–	–
Testes (mm)	0·5–1·8 × 0·5–1·5	diam. 1·25	–
Ovary (mm)	0·5–0·9 × 0·4–1·2	–	–
Uterine field/length × 100(%)	11–15	16	10–15
Egg-length (μm)	80–120 (usually 90–110)	110–115	*c.* 110
Egg-shell thickness (μm)	4–10 (usually 6–8)	7–8	*c.* 7–8

subcylindrical (Figs 3A & 4) and slightly dorso-ventrally flattened. There is evidence to indicate that the host may affect not only the size, but possibly also the appearance of the worm. The body-surface is smooth, although contraction may cause superficial transverse folding. The *oral sucker* is ventrally subterminal, as there is a relatively well-developed but not distinctly glandular pre-oral lobe, and significantly smaller than the *ventral sucker*, which usually protrudes. The forebody is relatively short, especially in the larger specimens, as the hindbody grows at a much faster rate than either the forebody or the suckers.

The structure of the body-wall is simple. There is a thick tegument beneath which is a region of relatively dense, but small, circular muscle-bundles, and beneath this lies a thick longitudinal muscle-layer. The structure of the body-wall is similar in both fore- and hindbodies, but with an additional layer of relatively large diagonal muscle-bundles lying within the longitudinal muscle-layer in the forebody.

There is no prepharynx. The well-developed *pharynx* gives rise to a very short, posteriorly or dorsally oriented oesophagus, which divides into two antero-laterally directed branches. These initial branches have a cuticular lining similar to that of the oesophagus. Laterally to the pharynx these two branches give rise to the gut-caeca which turn and run posteriorly in the dorso-lateral field, following a relatively straight to sinuous course, and end blindly near the posterior extremity. There are no 'Drüsenmagen' in the 'shoulder-region' of the gut. The gut-caeca, which are slightly diverticulate, are often fairly narrow and possess a thick, villous lining.

The *excretory vesicle* is Y-shaped. The terminal pore leads into a long stem which divides, giving rise to antero-laterally oriented arms, between half to two-thirds of the total body-length from the anterior end. This position normally corresponds to the posterior half of the post-testicular region of the vitelline field or just posterior to the vitellarium. The arms, which are slightly diverticulate, extend forward laterally into the forebody where, as can be seen in our sectioned material, they unite via a narrow commissure anterodorsally to the oral sucker (Fig. 3B).

Two oval, post-ovarian *testes* occur in tandem or slightly obliquely, usually well anterior to the middle of the body. The posterior testis is often slightly larger than the anterior. The vasa efferentia lead anteriorly from the testes, pass into the forebody and unite immediately anteriorly to the ventral sucker as they pass through the posterior wall of the prostatic sac. Within this large, ova

Fig. 4 *Otodistomum veliporum* ex *Dalatias licha*: (A) from SW of Barra Head, Scotland; (B) from Bay of Biscay. (These figures are directly comparable with the figures of *O. cestoides* in Fig. 6.) Scale: 10 mm.

sac (Fig. 3B) the male duct widens to become a seminal vesicle. This elongate, oval organ may be slightly arcuate and extends antero-ventrally to about the middle of the prostatic sac, where it narrows and joins the pars prostatica. The latter duct possesses a villous lining and a dense covering of gland-cells which fill all the available space within the prostatic sac. It initially turns and runs postero-dorsally, before passing towards the anterior region of the prostatic sac, where it passes through the thin, muscular wall of the prostatic sac and assumes the form of an ejaculatory duct. This duct is very long and usually convoluted, eventually leading into a well-developed and conical permanent *sinus-organ*. The sinus-organ is situated within a normally deep genital atrium, the pore of which opens mid-ventrally just posteriorly to the level of the pharynx. Near to the distal extremity of the sinus-organ, the ejaculatory duct unites with the metraterm to form a short hermaphroditic duct which opens terminally (Fig. 3B). The convoluted nature of the ejaculatory duct, the size of the sinus-organ and genital atrium and to some extent the position of the genital pore, are all variable.

The oval *ovary* is medially or sub-medially situated immediately anteriorly to the testes. Anteriorly from it leads a short oviduct, which enters a large Mehlis' gland, within which it receives firstly Laurer's canal and then, widely separated, the common vitelline duct (Fig. 3C). Laurer's canal is simple, tubular and opens to the exterior dorsally to the ovary. The eggs are formed within Mehlis' gland. The *uterus* is entirely pre-testicular and rarely reaches posteriorly to the ovary. Its main bulk, coiled between the ovary and the ventral sucker, occupies less than 20% of the total body-length and normally only 10–15% in mature specimens. The first coils of the uterus act as a uterine seminal receptacle, the only seminal store in the female system. Dorsal to the ventral sucker the uterus narrows, follows a sinuous or direct course anteriorly, passing ventrally or ventro-laterally to the prostatic sac, where it gradually narrows and becomes the metraterm, which unites with the ejaculatory duct within the sinus-organ. The eggs, which lack spines or filaments, and possess a relatively thick shell, occur in great numbers within the uterus. The *vitellarium* is in the form of numerous follicles in two lateral fields, which usually extend from about the middle of the uterine field, or just posterior to this, to a level just inside the posterior half of the body, very rarely extending into the posterior third of the body. The lateral fields of follicles tend to be more medially situated posteriorly to the gonads and are often confluent in this region. There is a good deal of variation with regard to both the anterior and posterior limits of the vitellarium and in regard to the degree of confluence of the vitelline fields in the post-testicular region.

Discussion. One interesting feature of this species is that, not only is it absent from rays (Rajiformes), but, like the other species of *Otodistomum*, it does not occur in the adult form in galeomorph sharks. Mühlschlag (1914) and Maclaren (1903b) have recorded specimens of *Otodistomum* from the carcharhiniform galeomorph sharks *Scyliorhinus caniculus* and *Mustelus laevis*, respectively; but on both occasions they occurred encysted in the stomach wall. This indicates that some kind of host-specificity is involved, for many of these sharks and rays occupy similar ecological niches and feed on similar foods. Admittedly, there is an apparent ecological difference in that most of the hexanchiform and squaliform sharks which harbour *O. veliporum* tend to be more pelagic and less benthic than the hosts of *O. cestoides*; but this does not apply to *Torpedo* spp. or *Squatina* spp. A further indication that host-specificity is involved is that there appears to be no record of adult *O. veliporum* from hosts which harbour *O. cestoides*, even though both parasites occur in squaliform sharks.

Another interesting feature of this species, and indeed of the other species of *Otodistomum*, is the different sizes attained in different hosts. *O. veliporum* is capable of reaching a massive size in *Dalatias licha* and *Hexanchus griseus*, and yet the largest recorded size for specimens from *Squalus acanthias* appears to be 30 mm, recorded by Layman (1930) off Vladivostok. This effect is probably exaggerated by the paucity of records from *S. acanthias*. The size at which maturity occurs also appears to be affected by the host, for while both of Baird's two specimens of *Distoma microcephalum* (= *O. veliporum*), which measure 10 and 14 mm in length, contain large numbers of eggs, a specimen from *D. licha* of 13 mm was immature.

Otodistomum cestoides (van Beneden, 1871) Odhner, 1911

Distoma cestoides van Beneden, 1871.
Otodistomum cestoides pacificum Dollfus, 1937.
Distoma(um) veliporum Creplin of Olsson (1868a, 1868b, 1876), Lönnberg (1889a, 1889b, 1890, 1898), Linton (1898, 1901), Jägerskiöld (1900) and Sleggs (1927).
Otodistomum veliporum (Creplin) of Stafford (1904), Lebour (1908), Manter (1926), Lloyd (1938), Dawes (1946, 1947, in part), Rees (1953), Myers (1959, in part), Templeman (1973) and Brinkmann (1975, in part).
Otodistoma scymni (Risso) Guiart, 1938, in part.
Aphanhystera monacensis Guiart, 1938.
Otodistomum sp. of Williams & Richards (1966), Williams *et al.* (1970) and Manger (1972).

Type-host and locality. *Raja batis*, Belgian coast.

Records.

Table 7 Measurements of specimens of *Otodistomum veliporum* from various hosts taken from the literature. Figures

Author	Villot (1878)	Odhner (1911)	Mühlschlag (1914)	Dollfus (1937a)	Dollfus (1937a
Name used	*Distomum insigne*	*Otodistomum veliporum*	*Otodistomum veliporum*	*Otodistomum veliporum veliporum*	*Otodistomum veliporum leptotheca*
Host	*Echinorhinus brucus*	Sharks	Sharks	*Hexanchus griseus*	*Torpedo marmorata*
Locality	Roscoff, France	Mediterranean and South European Atlantic	?	Atlantic coast of France	Moroccan coa·
Number of specimens	?	?	?	5	2
Length (mm)	40–50 [35*]	up to 50	12–55	50–101	(25)–35
Breadth (mm)	6–10 [5·5*]	5–6	3·5–5·5	5·0–5·5	(3·5)–5·5
Forebody (mm)	–	–	–	–	(3·5)–?
Oral sucker (mm)	–	1·25–2 diam.	0·5–1·0 diam.	1·77–?	(1·2)–?× (1·5)–?
Ventral sucker (mm)	–	2–3·5 diam.	1–2 diam.	4·4–?	(2)–?× (2·5)–?
Sucker-ratio	–	(1 : 1·67)	(1 : 2)	(1 : 1·9)	(1 : 1·67)
Pharynx (mm)	–	–	–	–	(0·5)–?× (0·4)–?
Prostatic sac (mm)	–	–	–	–	(1·2)–?× (1·0)–?
Testes (mm)	–	–	–	–	(0·9)–?× (1·4)–?
Ovary (mm)	–	–	–	–	(0·7)–?× (0·8)–?
Uterine field/ length × 100 (%)	–	–	(14)	–	(9·5)–?
Egg-length (μm)	90 × 70 [93–97 × 62–66*]	*c.* 86 × 60–63	90 × 53	110–130 × 69–92	82–88 × 62–70
Egg-shell thickness (μm)	4 [6–7*]	6	7	6–8	6–6·5

* Figures of Dollfus (1937).

parentheses were calculated from the measurements or diagrams given by these authors.

Dollfus (1937a)	Guiart (1938)	Kay (1947)	Tendeiro & Valdez (1955)	Bråten (1964)	Caballero & Caballero (1969)
Otodistomum veliporum pachytheca	*Otodistoma scymni*	*Otodistomum plicatum*	*Otodistomum veliporum*	*Otodistomum veliporum*	*Otodistomum veliporum*
Torpedo marmorata & T. torpedo	*Echinorhinus brucus*	*Hexanchus griseus*	*Torpedo torpedo*	*Dalatias licha*	*Squatina californica*
Morocco, Mauritania & Bay of Biscay	Atlantic, SW of Finistere	Washington State, U.S.A.	Portuguese coast	Oslo Fjord, Norway	California, U.S.A
7	13	51	2	6	5
11–29 (9·5–16)	28–52	8–83	51·8	up to 135	40
2·1–6 (2·25–2·9)	4–5	3–7·5	4·3	up to 11	4·9
2·0–2·5)	–	–	–	–	6·76
0·75 × 0·9– ·0)	–	0·9–1·5 diam.	2·2 diam.	–	1·41 × 1·46
1·5–1·7 × ·6–1·75)	–	1·3–2·4 diam.	3·7 diam.	–	2·35 × 2·67
1 : 2)	–	(1 : 1·5)	(1 : 1·67)	–	1 : 1·8
0·35–0·4 × ·35)	–	–	–	–	0·65 × 0·58
0·9 × 0·6– ·65)	–	average length 1·97	–	–	(1·8 × 0·85)
0·35 × 0·6– ·75)	–	average ant. 1·17 × 1·05 post 1·08 × 0·99	–	–	1·26–1·44 × 1·15–1·2
0·39–0·4 × ·56–0·6)	–	average 0·61 × 0·3	–	–	0·91 × 0·84
11–12)	–	(15)	–	–	(19·5)
3–130 × 5–75	–	*c.* 110 × 70	97–103 × 66–75	–	107 × 73
–10	–	7·5–8	7·7–9·6	–	thick

(i) Material studied

(a) From the NE Atlantic

Raja batis [stomach] West of Orkney Is (60 N, 03 W; depth 273 m; Sept., 1959). Collected by H. H. Williams. BM(NH) Reg. No. 1959.10.14.24.

Raja batis [?] Faxa-Floi, Iceland (Oct., 1966). BM(NH) Reg. No. 1976.5.12.47–56 (see Manger, 1972 : 163; as *Otodistomum* sp.).

Raja batis [stomach] West of Scotland. Rees Collection. BM(NH) Reg. No. 1976.4.12.23.

Raja batis [stomach] Between Flannan Is and St Kilda off west coast of Scotland (58°N, 08°W; depth 130–134 m; July, 1976). BM(NH) Reg. No. 1976.9.8.1–2.

Raja batis [stomach] Oslo fjord, Norway. Collected by Esmark. Zoologisk Museum, Oslo Cat. Nos. C.53 (collected 1868), C.54, C.56 (collected 1863) and C.57 (collected 1863).

Raja nidarosiensis [stomach] Trondheim, Norway. Zoologisk Museum Oslo Cat. No. C.55 (collected March, 1889; probably material of Lönnberg, 1891 : 71) and C.72 (collected Dec., 1900).

Raja radiata [?] Vesterhorn, Iceland (Oct., 1966). BM(NH) Reg. No. 1976.5.12.57–66.

Raja radiata [?] Isafjordhur, Iceland (Oct., 1966). BM(NH) Reg. No. 1976.5.12.57–66.

Raja radiata [stomach and pyloric duct] (immature specimens in pyloric duct) Aberdeen, Scotland (Oct., 1973). BM(NH) Reg. No. 1976.5.12.67.

Raja radiata [stomach] Off eastern Iceland (63 N, 11°W; depth 410–420 m; June, 1974). BM(NH) Reg. No. 1976.5.12.37–40.

Raja radiata [stomach] Viking Bank, off coast of Norway (61°N, 03°E; depth 120–138 m; July, 1976). BM(NH) Reg. No. 1976.10.12.1.

Raja radiata [stomach] Kristineberg, Sweden (Jan., 1971). Material of J. Thulin.

Raja spinicauda [stomach] Off eastern Iceland (63°N, 11°W; depth 410–420 m; June, 1974). BM(NH) Reg. No. 1976.5.11.7–29.

Centroscymnus coelolepis [stomach] SW of St Kilda (58°N, 10°W; depth 1090–1120 m; April, 1973). BM(NH) Reg. No. 1976.5.11.30–34.

Chlamydoselachus anguineus [?] Varangerfjord, Norway (1896). Material referred to by Lönnberg (1898 : 4) and Odhner (1911 : 517). Zoologisk Museum, Oslo Cat. No. C.64.

(b) From elsewhere

Raja jenseni [stomach] Grand Bank, Newfoundland, Canada. Collected by W. Templeman. BM(NH) Reg. Nos 1963.9.6.1–2 and 1965.7.30.1–8.

Raja jenseni [stomach] Northern NW Atlantic (Sept., 1967 and May, 1968). Collected by W. Templeman. BM(NH) Reg. No. 1968.12.6.41–48.

Raja richardsoni [stomach] Northern NW Atlantic (Sept., 1967 and May, 1968). BM(NH) Reg. No. 1968.12.6.31–40 (see Templeman, 1973 : 1831; as *O. veliporum*).

Raja sp. (? *griseocaudata*) [stomach] North of Falkland Is (47°S, 61°W; depth 272–300 m; July, 1928). BM(NH) Reg. No. 1975.3.14.42–45 (see Gibson, 1976 : 200).

Centroscyllium fabricii [stomach] Grand Bank, Newfoundland, Canada. Collected by W. Templeman. BM(NH) Reg. No. 1965.7.30.9–12.

(ii) NE Atlantic records from the literature

Raja batis [stomach] Storeggen (Aug.) and Varberg (? date), Sweden. Olsson (1868a : 22; as *Distoma veliporum*).

Raja batis [stomach] Bohuslän, Sweden (Summer, 1868). Olsson (1868b : 478; as *Distoma veliporum*).

Raja batis [oesophagus] Belgium. van Beneden (1871 : 17; as *Distoma cestoides*).

Raja batis [stomach; occ. intestine] Skagerrak at Bohuslän, Sweden (July, Aug.). Olsson (1876 : 13; as *Distoma veliporum*).

Raja batis [?] Kristineberg, Sweden (Aug.). Lönnberg (1889a : 68; as *Distoma veliporum*).

Raja batis [?] Kärnigo, Sweden (Dec.). Lönnberg (1889b : 48; as *Distoma veliporum*).

Raja batis [?] Bergen, Norway (July, Aug.). Lönnberg (1890 : 46; as *Distoma veliporum*).

Raja batis [?] Aberdeen, Scotland. Scott, T. (1909 : 77; as *Distoma cestoides*).

Raja batis [?] Kristineberg, Sweden (1898). Odhner (1911 : 516).

Raja batis [stomach] Aberdeen, Scotland. Nicoll (1913 : 194).

Raja batis [stomach] Galway, Ireland. Little (1929 : 26).
Raja batis [stomach] Faxa-Floi, Iceland (64°N, 23°W; Oct., 1966). Manger (1972 : 163; as *Otodistomum* sp.).
Raja clavata [stomach] Varberg, Sweden (July). Olsson (1868a : 22; as *Distoma veliporum*).
Raja clavata [stomach] Bohuslän, Sweden (Summer, 1868). Olsson (1868b : 478; as *Distoma veliporum*).
Raja clavata [stomach] Skagerrak at Bohuslän, Sweden (July, Aug.). Olsson (1876 : 13; as *Distoma veliporum*).
Raja clavata [stomach] East coast of Iceland (66°N, 11°W; depth 142 m; Aug., 1948). Rees (1953 : 18; as *Otodistomum veliporum*).
Raja fullonica [stomach] Bohuslän, Sweden (Summer, 1868). Olsson (1868b : 478; as *Distoma veliporum*).
Raja fullonica [stomach, occ. intestine] Skagerrak at Bohuslän, Sweden (July, Aug.). Olsson (1876 : 13; as *Distoma veliporum*).
Raja fullonica [?] Bergen, Norway (July, Aug.). Lönnberg (1890 : 46; as *Distoma veliporum*).
Raja lintea [stomach] Bohuslän, Sweden (Summer, 1868). Olsson (1868b : 478; as *Distoma veliporum*).
Raja lintea [stomach] Skagerrak at Bohuslän, Sweden (July, Aug.). Olsson (1876 : 13; as *Distoma veliporum*).
Raja nidarosiensis [stomach] Trondheim, Norway (March, 1889). Lönnberg (1891 : 71; as *Distoma veliporum*).
Raja radiata [stomach] Bohuslän, Sweden (Summer, 1868). Olsson (1868b : 478; as *Distoma veliporum*).
Raja radiata [stomach] Skagerrak at Bohuslän, Sweden (July, Aug.). Olsson (1876 : 13; as *Distoma veliporum*).
Raja radiata [stomach] Northumberland, England. Lebour (1908 : 49; as *Otodistomum veliporum*).
Raja radiata [stomach] British waters. Williams & Richards (1966 : 556; as *Otodistomum* sp.).
Raja radiata [stomach] Scottish waters. Williams, McVicar & Ralph (1970, 46; as *Otodistomum* sp.).
Raja sp. [?] Swedish coast. Jägerskiöld (1900 : 72; as *Distomum veliporum*).
Centroscymnus coelolepis [stomach] Golfe de Gascogne, France (45°N, 03°W; depth 1431m; July, 1903: 44°N, 02°W; depth 1483 m; August, 1903). Guiart (1938 : 23; as *Otodistoma scymni*).
Centroscymnus coelolepis [stomach] Off Portugal (39°N, 10°W; depth 1628 m; Aug., 1910). Guiart (1938 : 24; as *Otodistoma scymni*).
Chlamydoselachus anguineus [?] Varangerfjord, Norway. Lönnberg (1898 : 4; as *Distomum veliporum*).

Aspects of biology. As in the case of *O. veliporum* there appears to be little information available concerning the larval stages and early intermediate hosts of this species. It is confined to Manter's (1926) description of the non-ciliated miracidium. There is no evidence that a crustacean intermediate host is involved. Immature encysted specimens (metacercariae) of *Otodistomum* have been recorded from various marine fishes (see p. 196), but it is not known for certain to which species they belong.

If the life-history of the freshwater azygiids can be used as a guide, the rays and small sharks presumably acquire these parasites either by feeding directly upon the cercariae or by feeding on molluscs; but it would appear more likely that they become infested by feeding upon small fishes infested with metacercariae.

Previous descriptions. Lebour (1908 : 49; as *O. veliporum*); Odhner (1911 : 516); Layman & Borovkova (1926 : 11); Manter (1926 : 14); Linton (1940 : 107); Miller (1941 : 47); Gibson (1976 : 200).

Description (Figs 5 & 6). This description is based on specimens from several species of ray, but especially on material from *Raja spinicauda*, *R. batis*, *R. richardsoni* and *R.* sp. (? *griseocaudata*), and from the shark *Centroscymnus coelolepis*. Measurements taken from these worms are given in Table 8, and measurements from the literature in Table 9.

Fig. 5 *Otodistomum cestoides*: (A) whole-mount, ex *Raja spinicauda*; (B) sagittal section of forebody showing terminal genitalia, ex *R. spinicauda*; (C) lateral view of ovarian complex, ex *Raja* sp. (? *griseocaudata*). Scale: (A) 5 mm; (B, C) 500 μm.

Fig. 6 *Otodistomum cestoides* from various hosts: (A) *Raja richardsoni*; (B) *R. batis*; (C) *R. radiata*; (D) *R. jenseni*; (E) *R.* sp. (? *griseocaudata*); (F) *Centroscyllium fabricii*; (G) *Raja spinicauda*; (H) *Centroscymnus coelolepis*. (All are drawn to the same scale and are directly comparable to the figures of *O. veliporum* in Fig. 4.) Scale: 10 mm.

Table 8 Measurements of specimens of *Otodistomum cestoides* examined from various hosts.

Host	*Raja batis*	*Raja jenseni*	*Raja radiata*	*Raja richardsoni*	*Raja spinicauda*	*Centroscymnus coelolepis*	*Centroscyllium fabricii*	*Chlamydoselachus anguineus*
Number of specimens	12	8	12	9	12	7	7	1
Length (mm)	3–46	20–48	1·9–23	17–75	9–33	3·9–35	20–31	15
Breadth (mm)	1–5	1·5–3·3	0·4–3·4	1·7–5·5	1·25–4	1–5·5	3·2–3·7	2·2
Forebody (mm)	1–6	2·1–4·0	0·5–3·3	3·6–8·5	1·75–3	1·4·5	2·0–3·75	2·4
Oral sucker (mm)	0·45–2·0 × 0·35–2·0	0·75–1·2 × 0·82–1·25	0·22–1·25 × 0·23–1·3	0·95–1·8 × 1·0–1·95	0·85–1·6 × 0·92–1·55	0·53–1·8 × 0·53–1·6	1·1–1·25 × 1·1–1·5	1·1 × 1·2
Ventral sucker (mm)	0·55–2·8 × 0·45–2·8	1·0–1·6 × 1·1–1·6	0·3–1·8 × 0·34–1·8	1·5–2·6 × 1·5–2·6	1·4–2·25 × 1·35–2·25	0·68–2·5 × 0·7–2·4	1·55–1·9 × 1·5–2·4	1·9 × 1·7
Sucker ratio	1 : 2·15–1·6	1 : 1·3–1·4	1 : 1·2–1·6	1 : 1·25–1·6	1 : 1·3–1·5	1 : 1·25–1·5	1 : 1·3–1·6	1 : 1·4
Pharynx (mm)	0·23–0·9 × 0·15–0·8	0·38–0·6 × 0·35–0·5	0·12–0·68 × 0·07–0·6	0·4–0·7 × 0·44–0·7	0·4–0·7 × 0·35–0·6	0·12–1·1 × 0·15–1·2	–	0·6 × 0·5
Prostatic sac (mm)	up to 1·4 × 1·2	0·7–1·4 × 0·4–0·9	up to 1·2–1·1	0·6–2·0 × 0·45–1·0	up to 1·3 × 0·75	0·16–1·5 × 0·18–1·0	–	–
Testes (mm)	0·1–1·7 × 0·1–1·2	0·6–1·5 × 0·55–1·4	0·04–1·1 × 0·04–1·4	up to 2·0 × 1·75	0·6–1·25 × 0·6–1·25	0·12–1·1 × 0·15–1·25	0·5–1·75 × 0·9–1·1	*c.* 0·6 × 0·6 –
Ovary (mm)	up to 1·2 × 1·2	0·4–0·8 × 0·45–0·9	0·04–0·6 × 0·04–1·0	up to 1·0 × 1·2	0·4 × –0·8 0·4–1·0	0·1–0·7 × 0·1–1·0	–	–
Uterine field/length × 100 (%) (mature specimens only)	17–28	12·5–29	18–36	19–37	16–33	17–21	18–40	27
Egg-length (μm)	67–87	58–94	59–95	68–100	72–100	72–97	74–102	*c.* 75–90
Egg-shell thickness (μm)	3–7 (usually 3–4)	3–6	2·5–5	3·5–5	3–6	3–4	3–6·5	–

The body of this often large, elongate worm is subcylindrical, being slightly dorso-ventrally flattened and attenuated towards both extremities (Figs 5A & 6). The body-surface is smooth, although transverse folds do occur in contracted material. The subterminal *oral sucker* is about two-thirds to three-quarters the size of the slightly protruding *ventral sucker*. There is a very distinct pre-oral lobe which is unusual in that it contains a dense concentration of gland-cells, though this is much less apparent in the specimens from *C. coelolepis*. The forebody is short, especially in the larger specimens, as it apparently grows at a much slower rate than the hindbody. The structure of the body-wall is similar to that of *O. veliporum*.

There is no prepharynx, the oral aperture opening directly into a well-developed *pharynx*. The relatively short oesophagus passes dorsally and divides, giving rise to two very short lateral branches lined with a cuticle similar to that of the oesophagus itself. These in turn give rise antero-laterally to the gut-caeca which pass posteriorly in the dorso-lateral fields, following a straight or sinuous course, and end blindly near the posterior extremity. There are no 'Drüsenmagen'. The relatively narrow gut-caeca have a villous lining and tend to be slightly diverticulate.

The *excretory system* is Y-shaped, the terminal pore leading into a long, slightly diverticulate stem which bifurcates just posteriorly to the testes in the anterior half of the post-testicular region of the vitellarium. The two arms pass antero-laterally and into the forebody where they re-unite antero-dorsally to the oral sucker (Fig. 5B).

The two oval, post-ovarian *testes* lie in tandem or slightly obliquely in about the middle of the body. The posterior testis is often slightly larger than the anterior. The vasa efferentia unite just anteriorly to the ventral sucker as they pass through the posterior wall of the prostatic sac (Fig. 5B). This large, oval sac has a thin, muscular wall and contains the seminal vesicle which is tubular, broad and usually very arcuate, often being almost U-shaped. The length of the seminal vesicle is variable, and, although it is often the same length as the prostatic sac, it is sometimes considerably shorter. It leads into a tubular pars prostatica which passes posteriorly dorsal to the seminal vesicle, before reflexing and passing anteriorly. The pars prostatica has a villous lining and a dense covering of gland-cells which fill the prostatic sac. As the male duct passes through the anterior wall of the prostatic sac it assumes the form of an ejaculatory duct. This part of the duct is very long, has a thick, muscular wall and is usually coiled between the anterior extremity of the prostatic sac and the base of the *sinus-organ*. Towards the distal extremity of the conical sinus-organ the ejaculatory duct unites with the metraterm to form a short hermaphroditic duct which opens terminally. The genital atrium is usually relatively deep and possesses a thick, muscular wall. The genital pore is mid-ventral, usually a short distance posterior to the pharynx. The degree of coiling of the ejaculatory duct and the size and shape of the sinus-organ and the genital atrium are all extremely variable (see Gibson, 1976 : fig. 6).

The oval *ovary* lies medially or sub-medially immediately anterior to the testes. From it a short oviduct leads directly into a relatively large compact Mehlis' gland situated antero-dorsally to the ovary. Within Mehlis' gland the oviduct receives first Laurer's canal and then, some distance along, the common vitelline duct (Fig. 5C). Laurer's canal is a simple tube, passing dorsally and opening to the exterior at about the level of the ovary. The first coils of the *uterus* act as a uterine seminal receptacle, this being the only seminal store in the female system. The uterus is almost entirely pre-ovarian, rarely reaching posteriorly to the ovary. The bulk of the uterine field occurs between the ovary and the ventral sucker, and accounts for between 17 and 40% (usually 20–30%) of the total body-length. As it passes into the forebody the uterus narrows and is less convoluted. It usually passes ventrally or ventro-laterally to the prostatic sac, where it narrows further and gradually assumes the form of a metraterm. Anteriorly to the prostatic sac the metraterm passes antero-dorsally and enters the sinus-organ, where it unites with the ejaculatory duct. Eggs without spines or filaments are formed within Mehlis' gland: these possess a shell which is not as thick as that of some of the other species of *Otodistomum*. The follicular *vitellarium* occurs in two lateral fields between a level which is usually a short distance anterior to the middle of the uterine field and a level approximately halfway between the posterior testis and the posterior extremity. The anterior and posterior limits of the vitellarium are, however, extremely variable. The posterior limit can, for example, be almost anywhere within the posterior third of the body. Posteriorly to the gonads the lateral fields of follicles tend to be confluent, but the degree of confluence is also variable.

Table 9 Dimensions of *Otodistomum cestoides* from various hosts taken from the literature. Figures given in

Authority	Lebour (1908)	Odhner (1911)	Manter (1926)	Linton (1940)[1] van Cleave & Vaughn (1941)[2]
Name used	*Otodistomum veliporum*	*Otodistomum cestoides*	*Otodistomum cestoides*	*Otodistomum cestoides*
Host	*Raja radiata*	*Raja* spp.	*Raja laevis*	*Raja laevis*
Locality	Northumberland coast, England	North Atlantic	Maine, U.S.A.	Massachusetts[1] New Hampshire[2] U.S.A.
Number of specimens	1	?	Many	Many
Length (mm)	32	up to 65	1·9–65 (33)	10–54[1] 6·9–30·2[2]
Breadth (mm)	2·6	3–5	0·56–3·5* (3·8)	2–4·5[1]
Forebody (mm)	–	–	0·93–5* (4·2)	–
Oral sucker (mm)	1·2 diam.	1·5–2	0·28–1·56* diam. (1·6 × 1·6)	–
Ventral sucker (mm)	2·4 diam.	2–2·75	0·39–2·31* diam. (2·2 × 2·4)	–
Sucker-ratio	1 : 2	1 : 1·35	(1 : 1·25–1·67)*	–
Pharynx (mm)	0·4 × 0·35	–	(0·6 × 0·4)	–
Prostatic sac (mm)	–	–	(0·9 × 0·7)	–
Testes (mm)	1·3–1·5 diam.	–	(1·0 × 1·0)	–
Ovary (mm)	1·2 diam.	–	(0·5 × 0·8)	–
Uterine field/ length × 100 (%) (mature only)	(*c.* 18)	–	(*c.* 20–42)*	–
Eggs (μm)	60	65–72 × 43	average 69·4 × 46·2	*c.* 78 × 51[1] 55–90 × 36–58[2]
Egg-shell thickness (μm)	–	3	*c.* 4·5	3[1] 3–4[2]

* Figures from specimens of 1·9 to 39 mm in length. † New measurements.

parentheses were calculated from the measurements or illustrations given in the literature.

Manter (1926)[1] Dollfus (1937a)[2] van Cleave & Vaughn (1941)[3]	Layman & Borovka (1926)	Miller (1941)	Guiart (1938)	Guiart (1938)	Gibson (1976)
Otodistomum veliporum[1] *Otodistomum cestoides*[2, 3]	*Otodistomum cestoides*	*Otodistomum cestoides*	*Otodistoma scymni*	*Aphanhystera monacensis*	*Otodistomum cestoides*
Raja binoculata	*Raja radiata*	*Raja laevis*	*Centroscymnus coelolepis*	*Centroscymnus coelolepis*	*Raja* sp. (? *griseocaudata*)
Pacific coast of U.S.A.	Barents Sea	Atlantic coast, Canada	Gulf of Gascogne	Off Monaco	Patagonian shelf
Many	14	3	16	3	10
3–50[1], up to 61·5[2] 3·9–69[3]	39–52	up to 12·5	17·5–38 (17·5–27)	16–20 (17)	7·5–20
verage 3·81[1] p to 3·5[2]	3·3–3·9	up to 1·6	3–5·5 (3–3·5)	3·5–5 (3·5)	0·9–2·0
p to *c.* 9[2]	–	1/5 body-length	(3·2–4·8)	(3·2)	–
·77[2]	0·9–1·4 × 1·18–1·59	up to 0·72 × 0·79	(1·2–1·4 × 0·95–1·6)	(*c.* 1·0 × 1·0)	0·65–1·1 × 0·65–1·1
·95[2]	2·13 × 2·05	up to 1·14 × 1·24	(1·7–2·25 × 1·7–2·4)	(2·25 × 2·25)	1·0–1·7 × 1·0–1·7
l : 1·67)[2]	(1 : 1·25–1·67)	(1 : 1·5)	(*c.* 1 : 1·67)	(*c.* 1 : 2)	1 : 1·25–1·67†
	0·52–0·56 × 0·59–0·66	0·31 length	–	–	0·35–0·4 × 0·25–0·35
	–	–	–	–	0·6–1·3 × 0·4–0·7
	1·38–1·89 × 1·23–1·64	–	–	–	0·6–1·2 × 0·3–1·2
	0·82–0·85 × 0·89–0·95	–	–	–	0·3–0·7 × 0·35–0·9
	(*c.* 30)	–	(*c.* 15–20)	–	18·5–30†
verage 85·5 × 57·8[1] ·5–73 × 41–49[2])–94 × 40–70[3]	82–98·5 × 49	(immature)	–	(immature)	74–89 × 50–59
4[1] 3–4[2] -5[3]	–	–	–	–	4–6

Discussion. One record, which apparently refers to *O. cestoides*, which should be commented upon is that of Lönnberg (1898) from the very rare hexanchiform shark *Chlamydoselachus anguineus* in a fjord in northern Norway, well outside the normal range of this fish. As *O. veliporum* is common in the related *Hexanchus griseus*, one might have assumed that Lönnberg's material, which he did not describe, also belonged to this species. However, Odhner (1911 : 517, footnote), presumably after examining the material, referred it to *O. cestoides*, and this was accepted by Dollfus (1937a). We had some doubts in accepting this record, for although it is possible that *O. cestoides* might occur in hexanchiform sharks, the life-style of *C. anguineus* is much more similar to the pelagic hosts of *O. veliporum* than to that of the squaliform hosts of *O. cestoides*. We have, however, examined the specimen referred to by Lönnberg and can confirm Odhner's determination (see Table 8). It is possible that this shark might have acquired this particular parasite accidentally by feeding upon an elasmobranch infested with *O. cestoides*.

Like *O. veliporum*, this species shows variation in development and size which seems to be affected by the host-species (see Fig. 6; Tables 8 & 9). Specimens from *Raja radiata* appear to mature at about 5–6 mm in length, whereas in specimens from *R. spinicauda* maturity apparently occurs at about 11 mm, which is similar to that found by Manter (1926), i.e. 11–15 mm, in material from *R. laevis*. Although our own specimens from *R. radiata* reached only 23 mm in maximum length, Layman & Borovkova (1926) recorded specimens of up to 52 mm. Specimens from *R. binoculata*, *R. laevis* and *R. richardsoni* often reach lengths of more than 50 mm, whilst Gibson (1976) recorded specimens from *Raja* sp. (? *griseocaudata*) of only up to 20 mm in length. Although the paucity of records, and the lack of knowledge of seasonal variation probably bias these results, it does appear that these worms reach a greater size in certain hosts, and they appear to mature at a smaller size in hosts which contain small worms. This suggests that some rays provide a more suitable habitat than others and, indeed, the total absence of this parasite from certain rays, such as *R. naevus* which has been examined in great numbers (500+) by McVicar (1973), adds additional weight to this hypothesis.

Otodistomum plunketi Fyfe, 1953

Type-host and locality. *Scymnodon plunketi*, Otago, New Zealand.

Records.

(i) Material studied.

Etmopterus princeps [body-cavity] East Rockall (57°N, 13°W; depth 1000–1060 m; June, 1974). BM(NH) Reg. No. 1976.5.12.3–4.

(ii) NE Atlantic records from the literature.

None.

Aspects of biology. Nothing is known about the life-history of this species. It is probably similar to that of the gastric species of this genus, with the exceptions that the encysted metacercariae must penetrate the gut-wall in order to grow in the body-cavity, and the the eggs must, presumably, be lost through the abdominal pore.

Previous descriptions. Fyfe (1953 : 187); Skrjabin & Guschanskaja (1958 : figure only).

Description (Fig. 7). Due to the very large size of these worms and their bowed shape when fixed, the following description is based mainly on the smallest of the three specimens found, this being the only one which could be mounted on a slide. Even so, the thickness of this specimen prevented much of the internal structure being observed. Parts of one of the larger specimens, showing details of the terminal genitalia, and the proximal part of the female system, were sectioned. The dimensions of the worms and measurements from the literature are given in Table 10.

The worms are large, oval and very flattened dorso-ventrally (Fig. 7A), being similar in shape to the anaporrhutine gorgoderids, which also inhibit the body-cavity of elasmobranchs. Two of the present specimens, fixed without any pressure, have assumed a concave shape with the whole of the uterine field protruding ventrally. The body-surface is smooth. The *oral sucker* is sub-

terminal and about two-thirds as large as the *ventral sucker*. There is a pre-oral lobe, which, although containing numerous nuclei, does not contain the great number of gland-cells which usually occurs in *O. cestoides*. The forebody is short, conical and much narrower than the hindbody (Fig. 7A). The structure of the body-wall is basically similar to that of *O. veliporum* and *O. cestoides*, except that the tegument and the muscle-layers are much thinner, as is usual in coelomic parasites.

Details of the *pharynx* and oesophagus could not be made out in the whole-mount, but sections show that there is no prepharynx, a large, oval pharynx and a short oesophagus, which passes dorsally before joining the caecal bifurcation. There are no 'Drüsenmagen', and the relatively narrow gut-caeca pass back sinuously and end blindly close to the posterior extremity. The terminal region of the caeca is especially sinuous and slightly diverticulate.

Some of the details of the *excretory system* could not be determined in this material, but the pore is terminal and the vesicle Y-shaped, bifurcating at about the level of the posterior testis, according to Fyfe (1953). Our sectioned material indicates that, contrary to the usual condition in *Otodistomum* spp., the excretory arms, which are very diverticulate, end blindly on each side of the body dorso-laterally to the oral sucker. This latter feature is visible in the figure given by Skrjabin & Guschanskaja (1958).

Table 10 The dimensions of *Otodistomum plunketi*.

Authority	Fyfe (1935)	Skrjabin & Guschanskaja (1958)	Present material		
Host	*Scymnodon plunketi*	*Raja longirostris*	*Etmopterus princeps*		
Locality	Off New Zealand	Pacific coast of U.S.S.R.	East Rockall		
Number of specimens	30	? (1)	3		
Length (mm)	46–82	(*c.* 55)	27	*c.* 38	*c.* 42
Breadth (mm)	27–33	(*c.* 19)	14	20	21
Forebody (mm)	–	(*c.* 8)	3.1	–	–
Oral sucker (mm)	3·0–3·9 diam.	(*c.* 2·5) diam.	1·17 × 1·52	–	–
Ventral sucker (mm)	4·0–5·19 diam.	(*c.* 3·5) diam.	2·1 × 2·6	–	–
Sucker ratio	(1 : 1·5)	(*c.* 1 : 1·5)	1 : 1·7	–	–
Testes (mm)	2·5 × 3·0	(*c.* 1·5) diam.	0·8 × 1·5	–	–
Ovary (mm)	1·88 × 2·63	(*c.* 1·5 × 2·5)	*c.* 1·0 × 1·2	–	–
Uterine field/length × 100 (%)	(*c.* 40)	(*c.* 33)	40	–	–
Egg-length (μm)	111 × 75	–	102–118 × 70–80	–	–
Egg-shell thickness (μm)	9	–	6–8	–	–

The figures in parentheses were taken from an illustration in the literature.

The two *testes* are oval and situated obliquely about two-thirds of the body length from the anterior end. Details of the terminal genitalia are not clearly visible in the whole-mount, but are very distinct in the sections. The seminal vesicle, as in other azygiids, is broad, tubular, curved and, along with the tubular pars prostatica, contained in the oval prostatic sac (Fig. 7B). This latter organ, which measures about 2 × 1 mm in the sectioned specimen, is situated immediately anteriorly to the ventral sucker. The two vasa efferentia pass through the wall of the prostatic sac a short distance apart and not in union, as is the case in *O. veliporum* and *O. cestoides*. A long convoluted ejaculatory duct leads from the prostatic sac into a large, muscular conical *sinus-organ*. The fusion of the ejaculatory duct and metraterm occurs near the distal extremity of the

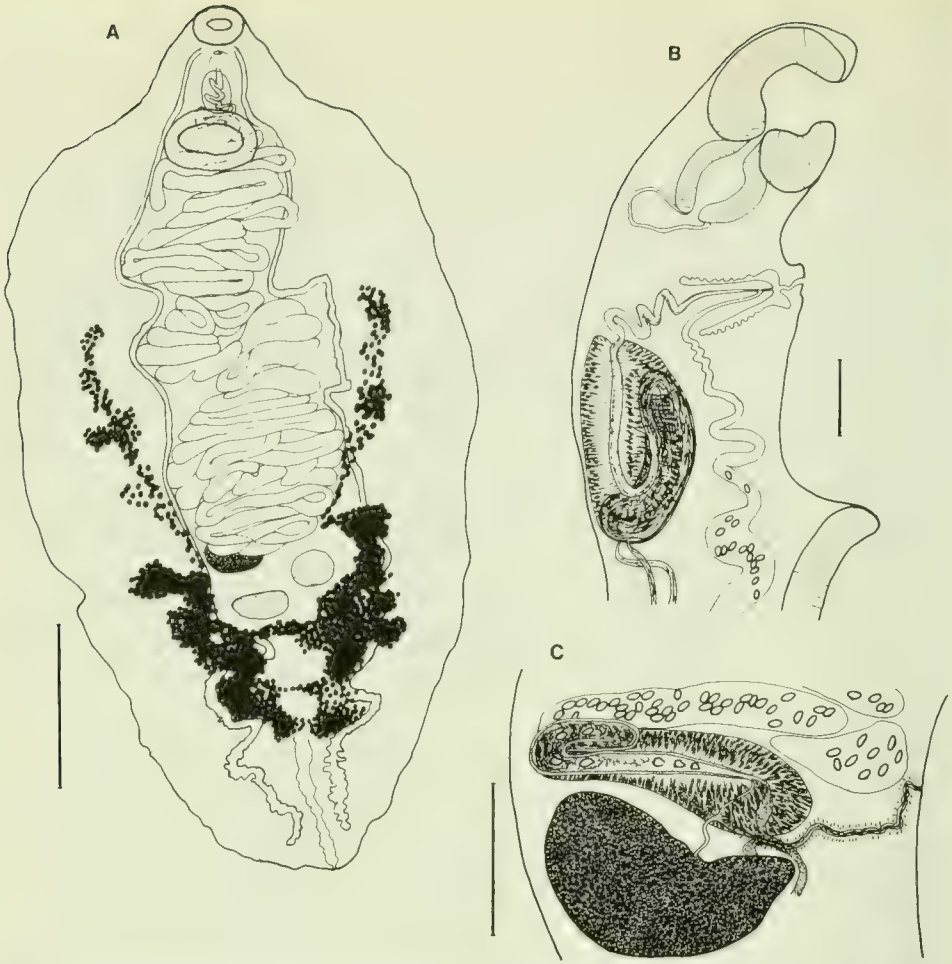

Fig. 7 *Otodistomum plunketi* ex *Etmopterus princeps*: (A) whole-mount; (B) sagittal section of fore-body; (C) lateral view of ovarian complex. Scale: (A) 5 mm; (B, C) 1 mm.

sinus-organ, and a very short hermaphroditic duct, opening terminally, is formed. There is no sinus-sac. The genital atrium is large, but almost completely filled by the sinus-organ, and the genital pore is situated mid-ventrally just posteriorly to the pharynx.

The *ovary*, which is apparently sometimes larger than the testes, is oval and almost immediately pre-testicular. A short oviduct leads anteriorly directly into a large, oval Mehlis' gland (Fig. 7C). Just within Mehlis' gland the oviduct unites with Laurer's canal. Towards the centre of Mehlis' gland, some distance from its union with Laurer's canal, the oviduct receives the common vitelline duct, and almost immediately dilates to form the oötype, which continues as the uterus. The first part of the *uterus* contains spermatozoa and thus acts as a uterine seminal receptacle. Laurer's canal is tubular and, although it may be slightly dilate proximally and contain spermatozoa and vitelline material, it does not appear to form a distinct rudimentary seminal receptacle as figured by Fyfe (1953). This canal, which has a thick wall and is surrounded by gland-cells, opens dorsally at the level of Mehlis' gland. The uterus does not reach posteriorly to the ovary,

but coils inter-caecally between the ovary and the ventral sucker, occupying about 40% of the total body-length. Anteriorly to the ventral sucker the uterus narrows to form a metraterm, which unites with the ejaculatory duct within the sinus-organ. The numerous eggs, which are without spines or filaments, are large and possess thick shells. At the proximal extremity of the uterus the eggs are light brown in colour, as in other species of *Otodistomum*, presumably being untanned; but as they pass down the uterus they become darker. The follicular *vitellarium* occurs in two sublateral fields between a level just anteriorly to the middle of the uterine field and a level halfway between the testes and the posterior extremity. These fields are confluent in parts of the post-testicular region. This species differs markedly from *O. veliporum* and *O. cestoides* in that the extra-caecal region of the body is very wide, which means that the anterior half of the vitelline field is isolated and not compressed between the body-wall and the uterine field.

Discussion. This species has been recorded previously from *Scymnodon plunketi* off New Zealand by Fyfe (1953) and *Raja longirostris* off the Pacific coast of the U.S.S.R. by Skrjabin, in Skrjabin & Guschanskaja (1958). Despite the opinions of Dawes (1946, 1947) and Brinkmann (1975), who apparently consider all of the species of *Otodistomum* of which they were aware to belong to a single variable species, *O. veliporum*, we believe that this species can be distinguished from the other species of the genus, except for *O. pristiophori* (Johnston, 1902) and *O. hydrolagi* Schell, 1972, by its location, the body-cavity, and by the broad shape of the body. *O. pristiophori* has been recorded from *Pristiophorus cirratus* in Australian waters by Johnston (1902) and Woolcock (1935) and from *Psammobatis microps* and *Squatina argentina* in the Atlantic ocean off northern Argentina by Ostrowski de Nunez (1971). *O. hydrolagi* was recorded from the chimaera *Hydrolagus colliei* off the Pacific coast of the U.S.A. by Schell (1972). *O. plunketi* differs from the other two remarkably similar species in its larger size, wider extra-caecal region of the body, longer uterine field, more posterior position of the gonads, and in the absence of a union of the excretory arms in the forebody. As few specimens of these coelomic forms of *Otodistomum* have been found, little is known of the morphological variability of these species. Further workers may in fact find that some or all of these forms tend to grade into one another, thus presenting similar problems to those of their gastric relatives.

Gibson & Bray (in preparation) suggest that the reason why adult helminths are fairly common in the coelom of elasmobranchs may have something to do with the fact that these fish possess an abdominal pore which permits the escape of eggs. Forms associated with this habitat tend to have a broad or spatulate body, sometimes in contrast to their near relatives from the gut. This may be an adaptation which has developed to prevent individual specimens being lost through the abdominal pore. Helminths from similar habitats, such as the urinary and swim bladders, where the relatively static conditions permit a reduction in sucker-size and where there is an outlet through which the parasite might be lost, tend to have similar adaptations.

Otodistomum sp. metacercaria

Distoma veliporum Creplin of Wagener (1852).
Otodistomum veliporum (Creplin) of Mühlschlag (1914, in part), Dollfus (1937a, in part), Ronald (1959, 1960), Olson & Pratt (1973), Scott, J. S. (1975).
Distoma (similar to *D. veliporum*) of Olsson (1868b).
Distoma nigrescens Olsson, 1876.
Agamodistomum chimaerae Ariola, 1899.
Xenodistomum melanocystis Stafford, 1904.
Distomum cestoides van Beneden of Scott, T. (1909).
Cercaria cestoides van Beneden of Nicoll (1913).
Otodistomum cestoides (van Beneden) of Nicoll (1913), Linton (1940, in part), Miller (1941, in part).
'Metacercaria' of Ruszkowski (1934).
Otodistomum (?) sp. of Manter (1934).

Records.

(i) Material studied

Coelorinchus caelorhinchus [encysted on liver] Off St Kilda (57°N, 10°W; depth 650–660 m; June 1974). BM(NH) Reg. No. 1976.5.11.54.

Conger conger [stomach] Skagerrak, 35–40″ NW of Hirtshals (depth *c.* 250 m; Sept., 1973). Material of J. Thulin.

Hippoglossoides platessoides [encysted in stomach wall] SW of Iceland (64°N, 24°W; depth 152–164 m; May, 1974). BM(NH) Reg. No. 1976.5.11.55.

Hippoglossoides platessoides [encysted in stomach wall] Off eastern Iceland (63°N, 11°W; depth 410–420 m; June, 1974). BM(NH) Reg. No. 1976.5.11.35–43.

Raja fyllae [encysted in stomach wall] East Rockall (57°N, 13°W; depth 800–820 m; June, 1974). BM(NH) Reg. No. 1976.5.11.44–53.

Rhinonemus cimbrius [liver] Gothenburg fish market (March, 1973); Skagerrak (Dec., 1970; Feb., 1971); Tjänö Marine Zoological Station, Bohuslän, Sweden (June, 1971). Material of J. Thulin.

(ii) From the literature

Chimaera monstrosa [encysted in wall of stomach and spiral intestine] Herdla, Norway. Ruszkowski (1934 : 487; as 'metacercaria'; see Dollfus, 1937a : 449 footnote).

Chimaera monstrosa [encysted in stomach wall] Bay of Setubal, Portugal (38°N, 09°W, depth 350 m; Nov., 1933). Dollfus (1937a : 447).

Chimaera monstrosa [encysted in wall of spiral intestine] Berlin Museum material, locality unknown. Mühlschlag (1914 : 200).

Glyptocephalus cynoglossus [encysted in stomach wall] Moray Firth, Scotland, Scott, T. (1909 : 77; as *Distomum cestoides* in *Pleuronectes microcephalus* – host corrected by Nicoll, 1915 : 360).

Glyptocephalus cynoglossus [stomach wall] Aberdeen, Scotland (Sept., 1908). Nicoll (1913 : 194; as *Cercaria cestoides* and *Otodistomum cestoides*).

Lophius piscatorius [stomach] Skagerrak, Sweden. Olsson (1868b : 477; as *Distoma* similar to *D. veliporum*: 1876 : 19; as *Distoma nigrescens*: see Dollfus, 1937a : 446).

Molva molva [branchial arch] Skaggerrak, Sweden. Olsson (1876 : 19; as *Distoma nigrescens*).

Previous descriptions. Ariola (1899 : 8; as *Agamodistomum chimaerae*); Nicoll (1913 : 194; as *Cercaria cestoides* and cercaria of *Otodistomum cestoides*); Manter (1934 : 324; as *Otodistomum* (?) sp.); Ruszkowski (1934 : 487; as 'metacercaria'); Dollfus (1937a : 447; as *Otodistomum veliporum* metacercaria); Linton (1940 : 108; as *Otodistomum cestoides*).

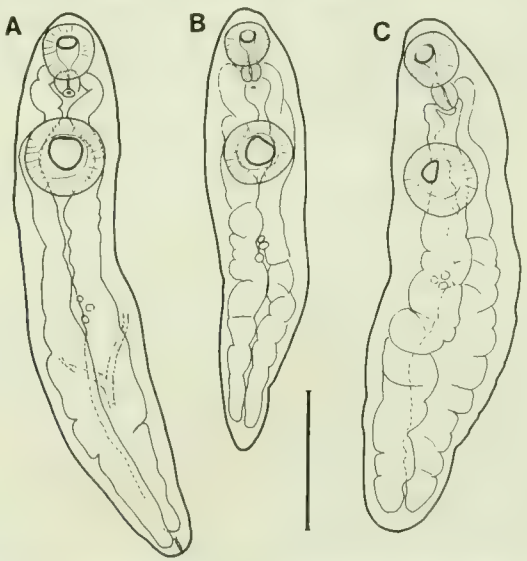

Fig. 8 *Otodistomum* sp. metacercariae: (A) ex *Coelorinchus caelorhinchus*; (B) ex *Hippoglossoides platessoides*; (C) ex *Raja fyllae*. Scale: 1 mm.

DESCRIPTION (Fig. 8). Morphologically these metacercariae are very similar to immature specimens of *O. cestoides* and differ from mature specimens in that the hindbody is much shorter in relation to the size of the forebody and the suckers (Fig. 8). The dimensions of the metacercariae are given in Tables 11 and 12.

Table 11 Dimensions of *Otodistomum* sp. metacercariae from various hosts.

Host	*Hippoglossoides platessoides*	*Coelorinchus caelorhinchus*	*Raja fyllae*	*Conger conger*	*Rhinonemus cimbrius*
Number of specimens	5	2	6	1	5
Length (mm)	1·9–4·1	4·5–5·6	2·35–3·8	7·6	1·76–6·5
Breadth (mm)	0·6–0·9	0·9–1·6	0·65–1·25	1·5	0·49–1·4
Forebody (mm)	0·6–1·0	0·8–1·1	0·52–0·95	2·1	0·59–1·5
Oral sucker (mm)	0·25–0·41 × 0·27–0·42	0·42–0·58 × 0·42–0·55	0·25–0·4 × 0·26–0·41	0·47–0·63	0·18–0·49 × 0·22–0·59
Ventral sucker (mm)	0·35–0·56 × 0·37–0·54	0·6–0·8 × 0·63–0·81	0·35–0·57 × 0·36–0·56	0·82–0·87	0·27–0·89 × 0·28–0·84
Sucker ratio	1 : 1·3–1·5	1 : 1·5	1 : 1·3–1·5	1·4	1·3–1·4
Testes (mm)	0·025–0·07 diam.	0·07–? diam.	0·035–0·07 diam.	0·13 diam.	0·03–0·11 diam.
Ovary (mm)	0·02–0·05 diam.	0·04–? diam.	0·025–0·05 diam.	–	up to 0·08 diam.
Uterine field/ length × 100 (%)	11–15	18–?	10–14	15	10–15

The metacercariae, which are surrounded by a host-tissue reaction in addition to their own cyst-wall, are usually elongate oval. One of the most noticeable features is the great breadth of the gut-caeca which may be more than half of the total body-width and thus overlap. The gonads are not always visible, but normally are very small. The distance between the ovary and the ventral sucker, the equivalent of the uterine field, is normally shorter than that of the adult specimens (cf. Fig. 2). No sign of any development of the vitellarium or the uterus is visible in whole-mounts, though the primordium of Mehlis' gland is often visible.

DISCUSSION. *Otodistomum* metacercariae have been attributed by various authors to both *O. veliporum* and *O. cestoides*. The only features of the key which can be applied to the metacercariae are the sucker-ratio and, to a limited extent, the presumptive uterine field (the distance between the ovary and the ventral sucker). The value of the latter feature is severely restricted for, as shown in Fig. 2, allometric growth is involved in its early development. The sucker-ratio of all the specimens we have measured and the majority of those in the literature (see Tables 11 & 12) strongly suggest that they belong to *O. cestoides*. In addition, the large size of the presumptive uterine field in some specimens tends to preclude the presence of *O. veliporum*, especially as further growth in this region would be expected as the worms mature. As shown in Figs 8 and 9 and Tables 11, 12 and 13, these metacercariae do tend to resemble immature specimens of *O. cestoides* from the definitive hosts.

The results of Linton (1940) are worth noting. He recorded *Otodistomum* metacercariae from *Alutera schoepfi*, *Lophius piscatorius* and *Palinurichthys perciformis*. The specimens from *A. schoepfi* were up to 13 mm long and possessed sucker-ratios, especially in the largest specimens, within the *O. veliporum*-range. *A. schoepfi* differs from the majority of hosts from which *Otodistomum* metacercariae have been recorded in that it is pelagic rather than benthic, and this corresponds to the preferred habitat of the majority of the definitive hosts of *O. veliporum* and contrasts with the benthic habit of the majority of the definitive hosts of *O. cestoides*. This ecological distinction is not clear-cut, however, as Linton also found large specimens from the benthic fish *Lophius piscatorius* which have a sucker-ratio on the border-line between the *O. veliporum* and

Table 12 Dimensions of *Otodistomum* sp. metacercariae recorded in the literature.

Authority	Ariola (1899)	Ruszkowski (1932)	Dollfus (1937a)	Nicoll (1913)	Manter (1934)
Name used	*Agamodistomum chimaerae*	'Metacercaria'	*Otodistomum veliporum* metacercaria	*Cercaria cestoides*	*Otodistomum* (?) sp.
Host	*Chimaera monstrosa*	*Chimaera monstrosa*	*Chimaera monstrosa*	*Glyptocephalus cynoglossus*	*Coelorinchus carminatus*
Locality	Genoa	Norway	Portugal	Aberdeen	Florida
Length (mm)	3·5–7	1·7–5·8	7·8–8·0	2·4	(3·55)
Breadth (mm)	–	0·5–1·0	1·6–1·8	0·66	(0·75)
Forebody (mm)	–	(1·2–1·5)	–	0·96	(0·9)
Oral sucker (mm)	*c.* 0·5 diam.	0·24–0·41 × 0·3–0·45	0·47 × 0·53	0·29 × 0·35	(0·28 × 0·3)
Ventral sucker (mm)	less than 1·0 diam.	0·36–0·68 × 0·37–0·67	0·85 × 0·79	0·43 × 0·59	(0·38 × 0·42)
Sucker-ratio	–	(1 : 1·3–1·5)	(1 : 1·5)	(1 : 1·7)	(1 : 1·4)
Uterine field/length × 100 (%)	–	(11)	(31)	–	(11)

Authority	Linton (1940)	Linton (1940)	Linton (1940)	Linton (1940)
Name used	*Otodistomum cestoides*	*Otodistomum cestoides*	*Otodistomum cestoides*	*Otodistomum cestoides*
Host	*Palinurichthys perciformis*	*Lophius piscatorius*	*Lophius piscatorius*	*Alutera schoepfi*
Locality	New England	New England	New England	New England
Length (mm)	4·34	3–4	8–10·5	2·24–13
Breadth (mm)	0·70	0·87–1·5	1·4–1·65	0·73–3·5
Forebody (mm)	–	–	–	–
Oral sucker (mm)	0·30 × 0·38	0·35 × 0·46–0·49	0·66–0·67 × 0·53–0·74	0·17–0·6 × 0·22–0·6
Ventral sucker (mm)	0·46 × 0·53	0·5 × 0·6–0·64	0·95–1·09 × 0·92–1·09	0·31–1·18 × 0·35–1·18
Sucker-ratio	(1 : 1·4)	(1 : 1·3–1·5)	(1 : 1·5–1·75)	(1 : 1·6–2·0)
Uterine field/length × 100 (%)	–	–	–	–

The figures in parentheses have been calculated from measurements or illustrations given by these authors.

Table 13 Dimensions of immature specimens of *Otodistomum veliporum* and *O. cestoides* from various hosts.

Species	*O. veliporum*	*O. cestoides*		
Host	*Dalatias licha*	*Raja batis*	*Raja radiata*	*Centroscymnus coelolepis*
Number of specimens	1	4	4	2
Length (mm)	13	3·0–5·1	1·9–5·5	3·9–5·0
Breadth (mm)	3	1·0–1·8	0·4–0·9	1·05–1·1
Forebody (mm)	1·7	1·0–1·2	0·53–1·07	1·05–1·1
Oral sucker (mm)	0·9 × 0·75	0·45–0·75 × 0·35–0·6	0·22–0·57 × 0·23–0·58	0·53 × 0·52–0·53
Ventral sucker	1·25 × 1·3	0·55–1·0 × 0·45–0·93	0·3–0·75 × 0·34–0·75	0·68–0·75 × 0·7
Sucker ratio	1 : 1·7	1 : 1·3 × 1·5	1 : 1·2 × 1·5	1 : 1·3
Testes (mm)	0·5 diam.	?–0·1 diam.	0·04–0·3 diam.	0·12–0·24 diam.
Ovary (mm)	–	–	0·04–0·2 diam.	0·1–0·13 diam.
Uterine field/ length × 100 (%)	12	*c.* 10–11	15–20	6–9

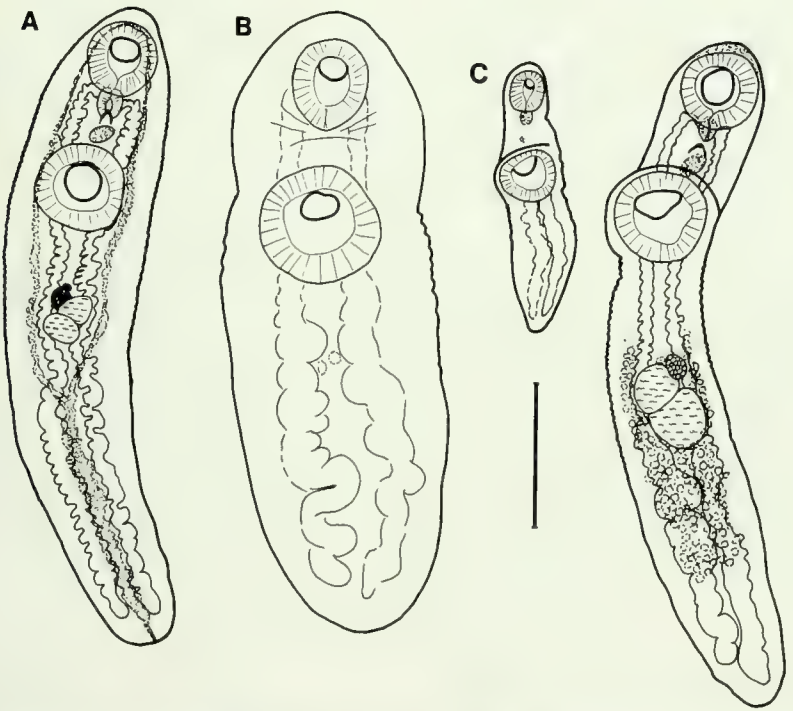

Fig. 9 Immature specimens of *Otodistomum cestoides*: (A) ex *Centroscymnus coelolepis*; (B) ex *Raja batis*; (C) two specimens ex *Raja radiata*. (These illustrations are directly comparable with those in Fig. 8.) Scale: 1 mm.

O. cestoides and a small specimen from the pelagic species *Palinurichthys perciformis* whose sucker-ratio fits well within the *O. cestoides*-range (Table 12). The large metacercariae, which may be *O. veliporum*, correspond with the large immature specimens of *O. veliporum* which we record from *Dalatias licha* (Table 13).

A further interesting result is recorded by Dollfus (1937a), who found specimens from *Chimaera monstrosa* off Portugal with a very large presumptive uterine field. Although they come within the range of *O. cestoides*, there is a possibility that they may be metacercariae of *O. plunketi*. The identity of this metacercaria is, however, further complicated by the existence of an adult coelomic form, *O. hydrolagi* Schell, in chimaeras.

We have referred to these metacercariae as *Otodistomum* sp., as we cannot with any confidence attribute them to any species of *Otodistomum*. We consider, however, that the vast majority of the forms recorded in the northeast Atlantic probably belong to *O. cestoides*.

Family **HIRUDINELLIDAE** Dollfus, 1932

Botulidae Guiart, 1938.
Lampritrematidae Yamaguti, 1940.
Mediolecithidae Oshmarin, 1968.

DIAGNOSTIC FEATURES. Body large; stout or elongate; very contractile. Body-surface smooth, may be papillate in forebody or around suckers and usually wrinkled transversely. Oral and ventral suckers well developed; latter well inside anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus usually short. Gut-caeca terminate blindly or form uroproct; may fuse subterminally forming a cyclocoel; usually diverticulate. Testes two; in tandem, oblique or symmetrical; pre-ovarian; in hindbody. Seminal vesicle tubular; normally thin-walled, occasionally anterior region may be thick-walled; convoluted in forebody. Pars prostatica well developed; tubular, usually long. Ejaculatory duct long; muscular; surrounded by muscular 'cirrus-sac'; opens into genital atrium through well-developed, conical or cylindrical 'cirrus'. Hermaphroditic duct, sinus-sac and sinus-organ absent. Genital atrium large, usually capable of being everted through genital pore. Genital pore mid-ventral in forebody. Ovary oval; post-testicular; in middle or anterior half of body. Laurer's canal and uterine seminal receptacle normally present (not reported in *Lampritrema*). Mehlis' gland post-ovarian. Juel's organ and canalicular or blind seminal receptacle absent. Uterus descends ventrally and ascends more dorsally; coiled mainly at level of vitellarium; but often extending more anteriorly into pre-ovarian region; mainly inter-caecal, occasionally reaching extra-caecally. Metraterm opens into genital atrium either directly or through a papillate organ immediately posterior to 'cirrus'. Eggs numerous; small; without filaments. Vitellarium composed of two to numerous long, straight or convoluted, branched tubules; mainly post-ovarian; inter- or extra-caecal. Excretory vesicle Y-shaped; stem short; arms initially in dorsal and ventral fields, very convoluted; unite in forebody. Parasitic in stomach (occasionally gills) of large, piscivorous teleosts.

COMMENT. Other workers, such as Yamaguti (1971), have considered that *Hirudinella* de Blainville, 1828, *Botulus* Guiart, 1938, and *Lampritrema* Yamaguti, 1940, form three distinct families. Our observations indicate that these three genera are morphologically very similar and, although we initially intended to distinguish *Lampritrema* at the subfamily level, we believe that the distinguishing features are not significant enough to be used at this level. We consider it likely, therefore, that the family Hirudinellidae consists, at present, of three monotypic genera.

Key to the genera of the Hirudinellidae

1 Body stout, elongate or 'key-hole' shaped; uroproct present; 'cirrus-sac' small, globular; seminal vesicle entirely thin-walled 2
– Body slender, very elongate; uroproct absent; 'cirrus-sac' large, elongate; distal part of seminal vesicle with muscular wall . . . . . ***Lampritrema*** Yamaguti, 1940 (p. 213)
2 Vitellarium in two lateral fields between level of testes and mid-hindbody; uterus mainly inter-caecal, post-ovarian, at level of vitellarium . . ***Hirudinella*** de Blainville, 1828 (p. 201)

– Vitellarium massed close to ventral surface, in single field, inter-caecally between ovary and posterior extremity; uterus reaching extra-caecally, mainly in anterior hindbody . . . . . ***Botulus*** Guiart, 1938 (p. 208)

HIRUDINELLA de Blainville, 1828

Hirudinella Garcin, 1730 [Pre-Linnaean; see Gibson, 1976]
Uroproctinella Skrjabin & Guschanskaja, 1957.

DIAGNOSTIC FEATURES. Body stout, elongate or 'key-hole' shaped. Body-surface often transversely wrinkled. Uroproct present; gut-caeca may fuse subterminally in old specimens forming cyclocoel. Testes symmetrical to oblique; in anterior hindbody. Seminal vesicle thin-walled throughout its length. 'Cirrus-sac' relatively small; globular. 'Cirrus' conical to digitiform. Genital atrium capable of being everted through genital pore. Ovary in anterior hindbody. Uterus mainly intercaecal; coils extending posteriorly from ovary to near posterior limit of vitellarium. Vitellarium in two lateral fields between testes and middle of hindbody. Parasitic in stomach of large, piscivorous marine teleosts (usually scombroids).

TYPE-SPECIES. *Hirudinella ventricosa* (Pallas, 1774) (by monotypy).

Hirudinella ventricosa (Pallas, 1774) Baird, 1853

Hirudinella marina Garcin, 1730.
Fasciola ventricosa Pallas, 1774.
Distomum ventricosum (Pallas) Monticelli, 1893.
Distomum ventricosum minor Shipley, 1900.
Fasciola clavata Menzies, 1791.
Distoma clavatum (Menzies) Rudolphi, 1808.
Hirudinella clavata (Menzies) de Blainville, 1828.
Fasciola fusca Bosc, 1802.
Distoma fuscum (Bosc) Poirier, 1885.
Hirudinella fusca (Bosc) Manter, 1926.
Fasciola coryphaenae Bosc, 1802.
Distoma coryphaenae (Bosc) Rudolphi, 1809.
Fasciola coryphaenae hippuridis Tilesius, in Rudolphi, 1809.
Fasciola scombri pelamidis Tilesius, in Rudolphi, 1809.
Distoma heurteli Poirier, 1885.
Distoma dactylipherum Poirier, 1885.
Distoma verrucosum Poirier, 1885.
Distoma personatum Poirier, 1885.
Distoma pallasii Poirier, 1885.
Hirudinella pallasii (Poirier) Guiart, 1938.
Distoma ingens Moniez, 1886.
Hirudinella ingens (Moniez) Darr, 1902.
Distomum validum von Linstow, 1886.
Brachylaemus validum (von Linstow) Stossich, 1892.
Distoma poirieri Moniez, 1891.
Hirudinella poirieri (Moniez) Dollfus, 1935.
Distoma siemersi Buttel-Reepen, 1900.
Hirudinella siemersi (Buttel-Reepen) Skrjabin & Guschanskaja, 1959.
Distoma ampullaceum Buttel-Reepen, 1900.
Hirudinella ampullacea (Buttel-Reepen) Skrjabin & Guschanskaja, 1957.
Hirudinella beebei Chandler, 1937.
Hirudinella spinulosa Yamaguti, 1938.
Uroproctinella spinulosa (Yamaguti) Skrjabin & Guschanskaja, 1957.
Hirudinella oxysoma Guiart, 1938.
Hirudinella phalloidea Guiart, 1938.
Hirudinella bonnacouri Guiart, 1938.
Hirudinella ahi Yamaguti, 1970.
Uroproctinella attenuata Hafeezullah, 1971.

TYPE-HOST. Unknown.

TYPE-LOCALITY. Amboyna, South China Sea.

RECORDS.

(i) Material studied

(a) From the NE Atlantic

None.

(b) From elsewhere

Acanthocybium solandri [stomach] Powell Islet, New Guinea (July, 1972). Collected by B. R. Smith. BM(NH) Reg. No. 1973.4.6.13–14.

Acanthocybium solandri [stomach] Zanzibar. Collected by J. F. C. Morgans. BM(NH) Reg. No. 1961.6.26.113–116.

Acanthocybium solandri [intestine] West Coast of Aldabra Atoll, Indian Ocean (Nov., 1974). Collected by C. R. Huxley. BM(NH) Reg. No. 1976.5.17.36–37.

Coryphaena hippurus [stomach] Between New Britain and New Ireland (Aug., 1972). Collected by B. R. Smith. BM(NH) Reg. No. 1973.4.6.12.

Euthynnus affinis [stomach] Cape Liguan, New Britain (May, 1972). Collected by B. R. Smith. BM(NH) Reg. No. 1973.4.6.5.

Euthynnus affinis [gut] Pondo harbour, New Britain (May, 1972). Collected by B. R. Smith. BM(NH) Reg. Nos 1973.4.6.4. and 1973.4.6.9–10.

Euthynnus affinis [stomach] East coast of South Africa (Dec., 1975). Collected by R. van der Elst. BM(NH) Reg. No. 1976.9.21.1.

Euthynnus alletteratus [gut] Port Moresby, New Guinea (Oct., 1971). Collected by B. R. Smith. BM(NH) Reg. No. 1973.4.6.8.

Katsuwonus pelamys [stomach] Locality (?). Unregistered.

Katsuwonus pelamys [gut] Gasmata, New Britain (Dec., 1971). Collected by B. R. Smith. BM(NH) Reg. No. 1973.4.6.1–3.

Katsuwonus pelamys [body-cavity] West Coast of Africa just north of Dakar, Senegal (19°N, 18°W; Oct., 1925). BM(NH) Reg. No. 1975.3.13.123 (see Gibson, 1976 : 232).

Naucrates ductor [?] North of Canary Isles (29°N, 15°W; depth 0–900 m; Oct., 1925). BM(NH) Reg. No. 1975.3.13.124 (see Gibson, 1976 : 232).

Neothynnus macropterus [stomach] Zanzibar (Aug., 1958). Collected by F. Williams. BM(NH) Reg. No. 1960.1.12.63–66.

Scomberomorus commerson [gut] New Guinea (June, 1972). Collected by B. R. Smith. BM(NH) Reg. No. 1973.4.6.11.

Scomberomorus commerson [stomach] NNW of Cape Liguan, New Britain (May, 1972). Collected by B. R. Smith. BM(NH) Reg. No. 1973.4.6.5.

Thunnus albacares [?] Mapelana, Natal, South Africa (May, 1975). Collected by R. van der Elst. BM(NH) Reg. No. 1975.9.17.20.

Thunnus albacares [stomach] Formosa Bay, North of Malindi, Kenya. BM(NH) Reg. No. 1969.11.11.3–4.

'Bonito' [?] Locality (?), BM(NH) Reg. No. 52.10.7.3.

'Bonito' [intestine] St Helena, SE Atlantic. Collected by A. E. Craven. BM(NH) Reg. No. 81.10.8.6–7.

'Dolphin' [liver] Atlantic Ocean. Collected by Capn Fraser. BM(NH) Reg. No. 95.11.15.1 (as *Distomum validum*).

'Kingfish' [stomach] Cosmoledo Is, Indian Ocean (Nov., 1952). BM(NH) Reg No. 1969.11.11.1–2.

Host (?) [?] Atlantic Ocean. BM(NH) Reg. No. 1914.1.22.2–4.

Host (?) [?] 'South of Europe'. BM(NH) Reg. No. 45.9.26.–.

Host (?) [?] Locality (?). BM(NH) Reg. No. 1914.1.22.1.

(ii) NE Atlantic records from the literature

Thunnus alalunga [stomach] Northern Bay of Biscay (47°N, 10°W; Sept., 1888). Guiart (1938 : 30; as *Hirudinella fusca*).

Thunnus alalunga [stomach] West of Cape Finistere, Spain (44°N, 13°W; July, 1888). Guiart (1938 : 31; as *Hirudinella poirieri*).

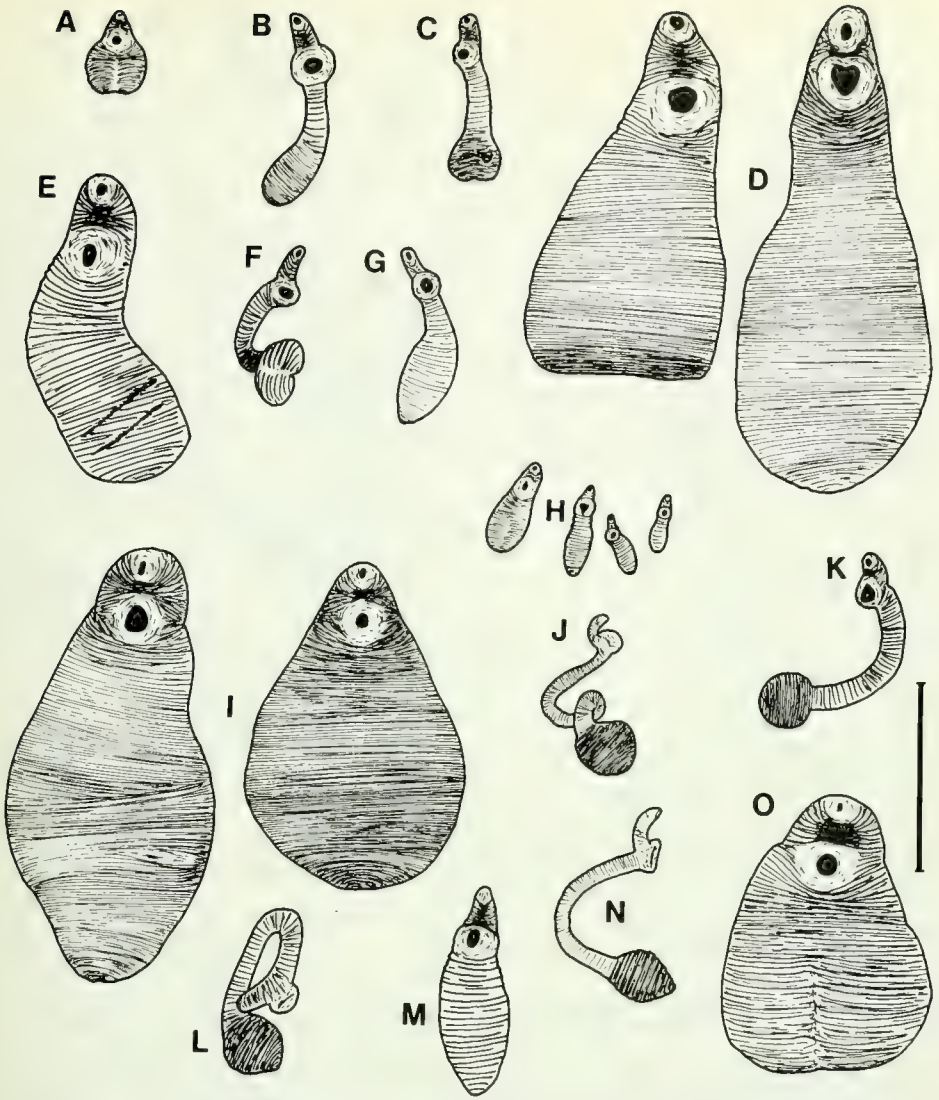

Fig. 10 Representatives of *Hirudinella ventricosa* from the collection of the British Museum (Natural History) to illustrate some of the variations in size and shape which occur in fixed specimens: (A) ex stomach of *Coryphaena hippurus* off New Guinea; (B) ex *Thunnus albacares* off Natal, South Africa; (C) ex intestine of *Katsuwonus pelamys* off St Helena; (D) two specimens ex stomach of 'Kingfish' off Cosmoledo Is, Indian Ocean; (E) ex unknown host from '? South of Europe'; (F) ex 'Bonito'; (G) ex unknown host from Atlantic Ocean; (H) four specimens ex stomach of *Thunnus albacares* off Zanzibar; (I) two specimens ex stomach of *Acanthocybium solandri* off Zanzibar; (J) ex gut of *Euthynnus affinis* off New Guinea; (K) ex stomach of *Scomberomorus commerson* off New Guinea; (L) ex gut of *Katsuwonus pelamys* off New Guinea; (M) ex 'Liver of Dolphin' from Atlantic Ocean (specimen labelled '*Distomum validum*'); (N) ex gut of *Euthynnus alletteratus* off New Guinea; (O) ex stomach of *Thunnus albacares* off Kenya. Scale: 20 mm.

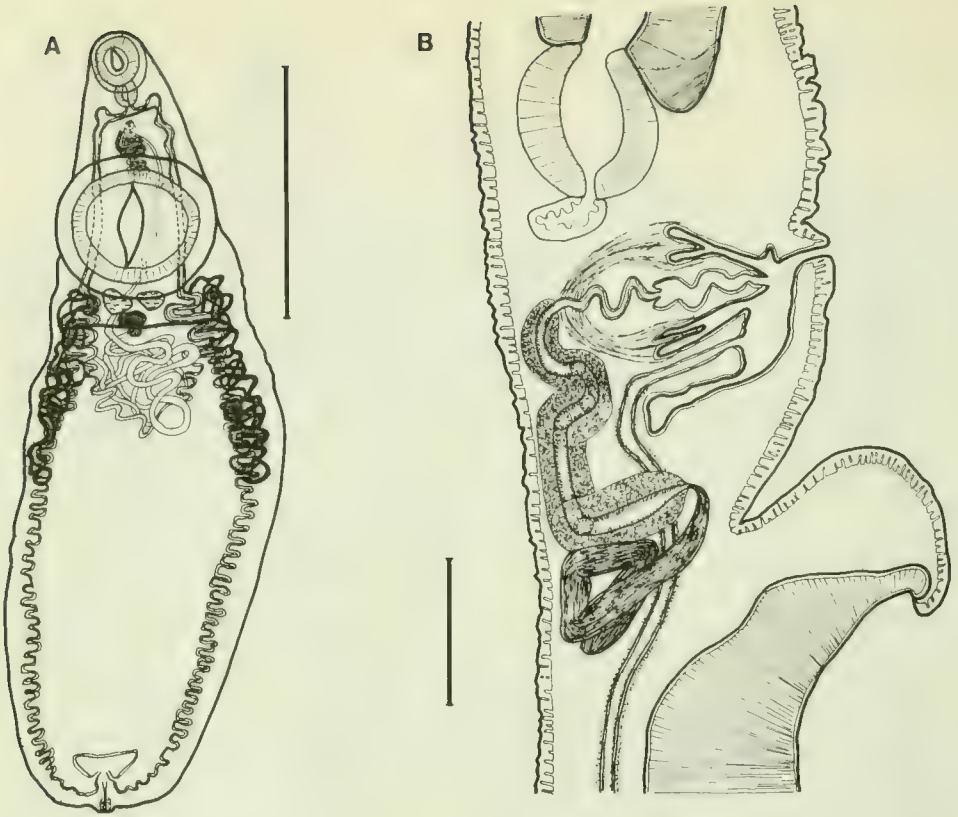

Fig. 11 *Hirudinella ventricosa* ex *Naucrates ductor* off Canary Isles: (A) internal details of worm reconstructed from sections; (B) sagittal section of terminal genitalia. Scale: (A) 10 mm; (B) 1 mm.

Thunnus alalunga [?] Concarneau, southern Brittany, France. Dollfus (1940 : 278; as *Hirudinella fusca*).

Thunnus alalunga [?] Golfe de Gascogne, Bay of Biscay. Aloncle & Delaporte (1970 : 297; 1973 : 568; 1974 : 10; as *Hirudinella fusca*).

Thunnas alalunga [?] Cote Cantabrique, Bay of Biscay, northern Spain. Aloncle & Delaporte (1970 : 297; as *Hirudinella fusca*).

Xiphias gladius [?] Norfolk, England (Aug., 1863). Cobbold (1867 : 200; 1883 : 404; as *Distoma clavatum*).

Although recorded from only two fishes in the northeast Atlantic region, it is likely that this parasite also occurs in *Katsuwonus pelamys*, *Euthynnus alletteratus*, *Coryphaena hippurus*, *Sarda sarda* and *Thunnus thynnus*, especially in the southern latitudes of this region. There are several 19th-century records of this parasite (see Nigrelli & Stunkard, 1947) from these hosts in the Atlantic Ocean, but the precise region is not listed.

Aspects of biology. The life-history of this species is not known. Aloncle & Delaporte (1970, 1973, 1974) have used this parasite as a 'biological tag'.

PREVIOUS DESCRIPTIONS. Poirier (1885 : 471; as *Distoma clavatum*, *D. verrucosum*, *D. pallasii*, etc.); Moniez (1886 : 531; as *D. ingens*); Buttel-Reepen (1900 : 586; 1902 : 175; as *D. ampullaceum* and *D. siemersi*); Darr (1902 : 670; as *D. clavata*); Mühlschlag (1914 : 232; as *D. ingens*); Chandler (1937 : 348; as *Hirudinella beebei*); Yamaguti (1938b : 40; as *H. spinulosa*: 1970 : 150; as *H. ahi* and *H. beebei*); Guiart (1938 : 28; as *H. phalloidea*, *H. fusca*, *H. poirieri* and *H.* sp.); Nigrelli & Stunkard (1947 : 189; as *H. marina* and *H. ventricosa*); Manter (1947 : 365); Hafeezullah (1971 : 76; as *Uroproctinella attenuata*); Gibson (1976 : 232).

DESCRIPTION (Figs 10 & 11). This giant species of digenean is very variable in both size and shape. Small fixed specimens, which are still large when compared to most other digeneans, tend to be elongate and usually possess a bulbous terminal portion (Fig. 10). The larger fixed specimens tend to be more robust and oval, but with the hindbody much broader than the forebody. Due to the great size of these worms, and the relatively weakly-muscled nature of the hindbody, larger specimens often become distorted during fixation, sometimes being flattened posteriorly or laterally where the specimens have rested on the base of the receptacle (Fig. 10D). Live specimens are reported to be extremely variable in shape. Nigrelli & Stunkard (1947), for example, note the following: 'Extended, it measures 170 mm long by 30 mm wide and it contracted to a length of only 40 mm . . . . When the worm was held up by the anterior end, the cecal contents passed to the posterior end which swelled in a balloon-like fashion. When placed in 10% formalin it contracted vigorously and when fixed it measured 98 by 40 mm. . . .'

The body-surface is smooth, although contracted live and fixed specimens are usually encircled by dermal folds (rugae). In addition, small papillae may be apparent, especially around the suckers. Beneath the thick tegument there is a thick interstitial matrix and several muscle-layers. A difference between the musculature of the body-wall in the fore- and hindbodies is apparent (see Gibson, 1976). In the forebody there are four layers of muscles: (1) circular; (2) outer longitudinal; (3) diagonal; and (4) inner longitudinal. In the hindbody, the outer layer of longitudinal muscles is very weakly developed and the diagonal muscles are very reduced and indistinguishable from the circular muscles which are reduced and sparse. The fibres appear to be hollow. The measurements of this species are given in Table 14.

The *oral* and *ventral suckers* are well developed, both being overlain by folds of the body wall. The oral sucker, which opens subterminally, is much smaller than the ventral sucker and the forebody is relatively short. There is no prepharynx, the well-developed *pharynx* is oval and the oesophagus short and narrow. The two gut-caeca each form a glandular sac (Drüsenmagen) in the 'shoulder'-regions, before running posteriorly. In the forebody, the caeca are usually relatively narrow and sinuous, but in the hindbody they dilate forming very large sac-like structures with small external diverticula (Fig. 11A). Close to the posterior extremity the caeca unite with the excretory vesicle through narrow ducts to form a uroproct. In mature specimens the caeca appear to be fused medially throughout much of the hindbody. In the majority of specimens the caeca contain the black residues of digesting blood.

The *excretory system* is very complex and difficult to follow, especially as the vesicle is almost obliterated by the giant sac-like gut. The terminal excretory pore leads into a (?) Y-shaped vesicle, the stem of which is probably short. The (?) two arms, which initially appear to be in dorsal and ventral fields, follow a very convoluted course extra-caecally throughout the hindbody. They pass into the forebody where they are sinuous, slightly wider and appear to unite dorsally to the oral sucker. This system is further complicated by the presence of two other much narrower systems of branching tubules (see Gibson, 1976): these may be branches of the excretory system or possibly a lymphatic system, a feature common in very large digeneans.

The two relatively small, oval *testes* are situated symmetrically just posteriorly to the ventral sucker (Fig. 11A). The small, tubular and convoluted seminal vesicle lies antero-dorsally to the anterior margin of the ventral sucker. This may be situated a little further forward, especially in immature forms, but its actual position depends somewhat upon the degree of contraction of the body. There is a long, tubular and convoluted or sinuous pars prostatica, which may be slightly wider in its mid-region. It is surrounded by a broad layer of gland-cells, which are strictly delimited by the surrounding tissue. There is a large, diffusely-muscled 'cirrus-sac', which surrounds the male terminal genitalia; this appears to be absent or very poorly developed in immature forms.

Table 14 Dimensions of *Hirudinella ventricosa* given in the literature.

Authority	Buttel-Reepen (1902)	Chandler (1937)	Yamaguti (1938b)	Manter (1947)	Nigrelli & Stunkard (1947)
Name used	*Distomum ampullaceum* *D. siemersi* *D. ingens*	*Hirudinella beebei*	*Hirudinella spinulosa*	*Hirudinella ventricosa*	*Hirudinella marina* *H. ventricosa*
Host	(?) *Coryphaena* sp. (?) *Sphyraena barracuda*	*Acanthocybium petus*	*Thunnus alalunga*	*Coryphaena hippurus*	Various scombriform fishes
Locality	(?) Indian and (?) Atlantic Oceans	Bermuda	Pacific Ocean	Tortugas, Florida	Various
Number of specimens	?	1	20	1	56
Length (mm)	33–60	32	up to 37	22·5	8·5–98
Breadth (mm)	16–22	19–20	up to 5·5	8·5	2–40
Forebody (mm)	–	–	–	–	–
Oral sucker (mm)	0·8–1·5 diam.	2·35 depth	1·12–1·7 diam.	1·74 diam.	2–4 diam. (not full range)
Ventral sucker (mm)	3–4 · 3	4 depth	2·5–3·6 diam.	3·88 diam.	3–7·5 diam. (not full range)
Pharynx (mm)	–	1·35 diam.	0·6–0·87 × 0·58–0·75	–	–
Testes (mm)	–	1·7 × 3–3·5	0·8–1·1 × 1·1–1·7	–	–
Ovary (mm)	–	1·5 × 2·5–3	0·8 × 1·0–1·7	–	–
Eggs (μm)	38–39·5 × 23	35–37 × 24–26	39–47 × 21–24	33 × 19	31–44 × 19·5–24

Authority	Yamaguti (1970)	Yamaguti (1970)	Yamaguti (1970)	Gibson (1976)
Name used	*Hirudinella ahi*	*Hirudinella beebei*	*Hirudinella marina*	*Hirudinella ventricosa*
Host	*Neothunnus macropterus*	*Acanthocybium solandri*	*Katsuwonus pelamys*	*Naucrates ductor*
Locality	Hawaii	Hawaii	Hawaii	Canary Isles
Number of specimens	1	2	5	1
Length (mm)	28	16–22	45–55	31
Breadth (mm)	4	5–6	5–7	10
Forebody (mm)	–	–	–	4·4
Oral sucker (mm)	1·15 × 1·7	1·0–1·2 × 1·3–1·6	1·3–1·7 × 1·4–2·0	1·45 × 1·3 (depth)
Ventral sucker (mm)	3·7 diam.	2·3–2·5 × 2·4–2·8	2·5–3·0 × 2·8–3·0	3·4 × 2·0 (depth)
Pharynx (mm)	0·6 diam.	0·6 diam.	0·7–0·85 × 0·55–0·75	0·8 diam.
Testes (mm)	0·56–0·8 × 0·8–1·1	0·33–0·41 × 0·3–0·54	0·5–1·0 × 0·4–0·85	1·1 × 0·8 (depth)
Ovary (mm)	0·75 × 0·95	0·13 × 0·25	0·5–0·9 × 0·5–0·75	0·5 × 0·3 (depth)
Eggs (μm)	35–42 × 18–24	39–42 × 23–26	23–33 × 18–23*	30–36 × 20–22

Due to the extreme morphological variability of this species, the value of this table is severely limited.
* 28–35 × 20–24 in live material.

As the male duct passes through the wall of the 'cirrus-sac', it assumes the form of an ejaculatory duct. This duct passes forward sinuously within the 'cirrus-sac' and into a well-developed conical 'cirrus', which projects into a large, wide genital atrium and may be surrounded by a small collar (Fig. 11B). The small genital aperture is situated mid-ventrally, close to the middle of the forebody.

The small, oval *ovary* is situated immediately posteriorly to the testes. Posteriorly to the ovary, Laurer's canal and the common vitelline duct unite with the oviduct prior to its entry into the small, oval Mehlis' gland. Laurer's canal opens dorsally, having followed a long, convoluted course. There is no blind or canalicular seminal receptacle. No spermatozoa were seen in the uterus of our sectional material, but as a uterine seminal receptacle was reported by Yamaguti (1938b) in his description of *H. spinulosa* and is present in the closely related genus *Botulus* (see below), we can be confident that it usually occurs. The *uterus* is coiled intercaecally in a space between the gonads and the anterior margin of the union of the gut-caeca in the hindbody. Dorsally to the posterior half of the ventral sucker the diameter of the uterus is reduced and it forms a metraterm which passes forward. Short villous projections line the metraterm, which is surrounded by small gland-cells. Just dorsally to the genital atrium, but posteriorly to the 'cirrus-sac', the metraterm loses its villous lining and outer gland-cells, acquires a cuticular wall and leads into the genital atrium through a finger-like process, which is often flattened distally (Fig. 11B). Whereas in mature specimens this female process is not closely associated with the 'cirrus', in immature forms, before the development of the 'cirrus-sac', these two organs may be fused over much of their length. Both male and female organs may be everted together through the genital pore (see Nigrelli & Stunkard, 1947 : Fig. 2); but they are usually withdrawn. The eggs, considering the size of the worm, are very small. According to Moniez (1891) and Nigrelli & Stunkard (1947), egg-size is correlated with the size of the worm, although Nigrelli & Stunkard present a table which does not show this correlation. Egg-size is, therefore, probably too variable to serve as a reliable specific character. The tubular vitellarium forms two regions lying extra-caecally and symmetrically, between the posterior margin of the ventral sucker and the middle of the body.

Discussion. The name *Hirudinella ventricosa* (Pallas, 1774) has been accepted by Gibson (1976) as the oldest available name for this species, as *H. marina* Garcin, 1730, is pre-Linnaean. Over the course of the past century there has been a certain amount of controversy over the number of species in this genus. Following the work of Moniez (1891) and Buttel-Reepen (1900, 1902), Nigrelli & Stunkard (1947), in their revision of the genus, considered that there were only two valid species, despite the large number of species attributed to the genus in the past. Recently, however, in line with the thoughts of some early workers, such as Cobbold (1879) and Blanchard (1891a, 1891b), Gibson (1976) has suggested that there is no substantial reason for accepting the presence of more than one species in the genus *Hirudinella*. We accept the latter opinion until there is substantial proof to indicate the presence of a second species. The great variability in shape and size appears to have led to the confused situation with regard to the taxonomy of the worm. The weak circular muscle in the hindbody and the fusion of the gut-caeca in the hindbody of larger individuals may account for the tendency they show to differ in shape from the smaller ones (Fig. 10). In addition, significant changes in the shape of the hindbody can be caused by differences in the orientation of the specimens or small changes in the contraction of the longitudinal musculature, when the voluminous gut-caeca are distended with the very fluid residues of digesting blood.

It is noticeable that there is a certain morphological similarity between *H. spinolusa* of Yamaguti (1938b) from *Thunnus alalunga*, *Uroproctinella attenuata* of Hafeezullah (1971) from *Neothunnus macropterus* and *H. marina* of Caballero y C. & Caballero R. (1971) from *Euthynnus lineatus*. Yamaguti claimed that his material possessed body-spines, Hafeezullah noted that spines were 'very sparse' and Caballero y C. & Caballero R.'s material was covered with digitiform papillae. We have examined material from *Euthynnus affinis* (Fig. 10J), *E. alletteratus* (Fig. 10N), *Neothunnus macropterus*, *Thunnus albacores* (Fig. 10H & O) and several other scombrids. Although some are morphologically similar to the specimens described by these authors, there is a variety of shapes present. Certainly papillae are apparent in certain specimens, especially around the oral and ventral suckers; but some of these papillae and the rugate nature of contracted material can present a spinulate appearance when viewed from certain angles, and it is possible that these papillae may be extensible under certain conditions. In addition, as pointed out by Gibson

(1976 : 234 footnote), the apparent spines in Yamaguti's material may have been caused by subtegumentary projections exposed after the loss of the tegument.

We have listed *Distomum validum* von Linstow, 1886, as a synonym of *H. ventricosa* despite the fact that it has been placed in *Brachylaemus* Dujardin, 1843, by workers such as Stossich (1892) and ('*sub judice*') by Yamaguti (1971), because the original description, although very incomplete, resembles the latter species very strongly. *D. validum* was described by von Linstow (1886) from a species of *Delphinus*. At first sight this appears to be a peculiar host for *Hirudinella*; but a search of the literature revealed that the original description of *D. pallasii* by Poirier (1885), a readily recognizable synonym of *H. ventricosa*, was based on material from *Delphinus phocaena* (= *Phocaena phocaena*). Similarly, *D. ampullaceum* Buttel-Reepen, 1900, was originally recorded from a cetacean. As it seems unlikely that a digenean parasite of teleosts could survive for long in a mammalian host, it must be assumed that these were accidental infestations acquired from the teleost-prey. There is, however, another possibility, as we consider that there may been have some confusion with regard to the common name of the host. The appellation 'dolphin', in addition to being the vernacular name for certain species of cetaceans, is also a vernacular name of the teleost *Coryphaena hippurus*, which is one of the normal hosts of *H. ventricosa*, and may have been applied by 19th-century fishermen to various scombroids. If the collector had recorded 'dolphin', then this would have been ambiguous for later workers. As an example, we have in the collection of the British Museum (Natural History) one specimen of *D. validum*, collected in the 19th century, the host of which is listed as 'dolphin'. The confusion between the vernacular names of *Coryphaena* and *Delphinus* has been appreciated for many years and was pointed out by Forster, in Osbeck (1771 : 117); but, although some authors now refer to *Coryphaena* as the 'dolphin-fish', this confusion still exists. For the above reason, Price (1932) did not include *Distoma validum*, *D. pallasii* or *D. ampullaceum* in his monograph on the trematode parasites of marine mammals.

BOTULUS Guiart, 1938

Profundiella A. S. Skrjabin, 1958.
Mediolecithus Oshmarin, 1968.

DIAGNOSTIC FEATURES. Body normally stout. Uroproct present. Testes symmetrical to oblique; in anterior hindbody; relatively large. Seminal vesicle thin-walled throughout its length. 'Cirrus-sac' relatively small; globular. 'Cirrus' conical to digitiform. Genital atrium often everted through genital pore. Ovary in anterior hindbody. Uterus reaching extra-caecally in anterior hindbody. Vitellarium a densely tangled mass of tubules in one ventral, inter-caecal field between ovary and posterior extremity. Parasitic in stomach of large piscivorous marine teleosts (*Alepisaurus*) and (?) accidentally in piscivorous sharks.

TYPE-SPECIES. *Botulus microporus* (Monticelli, 1889) n. comb. (by monotypy).

COMMENT. A certain amount of discussion has centred around the systematic position of *Botulus* and its synonyms. Giuart (1938) erected a new family, related to the Azygiidae and Hirudinellidae, for this genus. Stunkard (1965) considered the Botulinae to be a subfamily within the Hirudinellidae and synonymous with the Profundiellinae, which has been erected, within the Dinuridae, by A. S. Skrjabin (1958) for *Profundiella*. Yamaguti (1971) maintained the Botulidae as a distinct family, and recently Parukhin & Nikolaeva (1974) considered the Botulinae a subfamily within the Dinuridae and accepted the appelations Profundiellinae and Mediolecithidae, erected by Oshmarin (1968) for *Mediolecithus*, as synonyms. In our opinion (Gibson, 1976; Gibson & Bray, in preparation), *Botulus* is a monotypic genus within the Hirudinellidae which cannot be distinguished from *Hirudinella* and *Lampritrema* at the subfamily level. A main reason for recent major disagreements in the systematic position of *Botulus* is the erroneous descriptions of the terminal genitalia. Contrary to all the previous detailed descriptions of the genus, there is no sinus-sac or hermaphroditic duct present.

Botulus microporus (Monticelli, 1889) n. comb.

Distoma microporum Monticelli, 1889.

Apoblema microporum (Monticelli) Monticelli, 1891.
Hemiurus microporum (Monticelli) Looss, 1899.
Botulus alepidosauri Guiart, 1938.
Profundiella skrjabini A. S. Skrjabin, 1958.
Botulus skrjabini (A. S. Skrjabin) Parukhin & Nikolaeva, 1974.
Botulus cablei Stunkard, 1965.
Profundiella alepisauri Parukhin & Nikolaeva, 1967.
Botulus skrjabini alepisauri (Parukhin & Nikolaeva) Parukhin & Nikolaeva, 1974.
Mediolecithus pacificus Oshmarin, 1968.

TYPE-HOST AND LOCALITY. *Alepisaurus ferox*. Madeira,

RECORDS.

(i) Material studied
(a) From the NE Atlantic
Alepisaurus ferox [stomach] SE coast of Iceland. (depth 46 m). BM(NH) Reg. No. 1976.5.12.35–36.
(b) From elsewhere
Alepisaurus ferox [?] Madeira. Type-specimens of *Distoma microporum* Monticelli, 1889. BM(NH) Reg. No. 1914.4.22.1–6.
Alepisaurus ferox [stomach] Off Miami Beach, Florida. (Nov., 1964). Specimens donated by Dr R. M. Overstreet. BM(NH) Reg. No. 1976.5.11.3–6.
(ii) NE Atlantic records from the literature
None.

ASPECTS OF BIOLOGY. The life-history of *B. microporus* is not known. This species appears to be restricted to *Alepisaurus* spp., where they normally occur in the stomach. Oshmarin (1968), however, recorded a single specimen, which he named *Mediolecithus pacificus*, in the shark *Lamna cornubica*; but this, as Parukhin & Nikolaeva (1974) suggest, was probably an accidental infestation. Recently, Aleshkina (1976) claimed to have found *Botulus* sp. in *Thunnus obesus* from the 'equatorial and tropical' region of the Atlantic Ocean, and Parukhin (1976) records a specimen under the name *Botulus skrjabini* from the ovary of *Coryphaenoides striatura* off the east coast of Africa. As these worms were not described we do not know, assuming that they were correctly determined, whether they were adults or larvae, or whether these hosts were accidentally infested or form part of the life-history of this parasite. Aleshkina (1976) also records *Botulus* sp. from *Alepisaurus ferox* and *A. brevirostris* (as *A. breviductus*).

PREVIOUS DESCRIPTIONS. Monticelli (1889 : 322); Guiart (1938 : 26; as *Botulus alepidosauri*); A. S. Skrjabin (1958 : 340; as *Profundiella skrjabini*; English translation in K. I. Skrjabin & Guschanskaja, 1960 [1965] : 295); Stunkard (1965 : 488; as *Botulus cablei*); Parukhin & Nikolaeva (1967 : 757; as *Profundiella alepisauri*; 1974 : 117, as *Botulus skrjabini alepisauri*); Oshmarin (1968 : 272; as *Mediolecithus pacificus*).

DESCRIPTION (Fig. 12). These are very large, usually spindle-shaped worms; but they may vary between oval and almost cylindrical (Fig. 12), depending on the degree of contraction during fixation. They are circular or oval in cross-section. The relatively short forebody is much narrower than the hindbody: in some of the type-specimens the forebody is extended, thus giving the specimens an ampullaceous outline. In many specimens the oral sucker and pre-oral lobe form a short, subterminal, ventrally directed proboscis-like protrusion. The unarmed body-surface may be transversely wrinkled. The measurements of this species are given in Table 15.

As in *Hirudinella* the musculature of the body-wall differs in the fore- and hindbodies. In the forebody the muscle-layers occur as follows: (1) outer circular; (2) longitudinal; and (3) inner circular and/or diagonal. The inner layer of longitudinal muscles, present in *Hirudinella*, appears to be absent in *Botulus*. The musculature of the hindbody is similar to that in *Hirudinella*: there is a very poorly-developed layer of circular muscle, external to a narrow, but relatively well-developed, layer of longitudinal muscle.

A pre-oral lobe is present. The musculature of the well-developed oral and ventral suckers is overlain by the body-wall. The *oral sucker* is significantly smaller than the *ventral sucker*. The

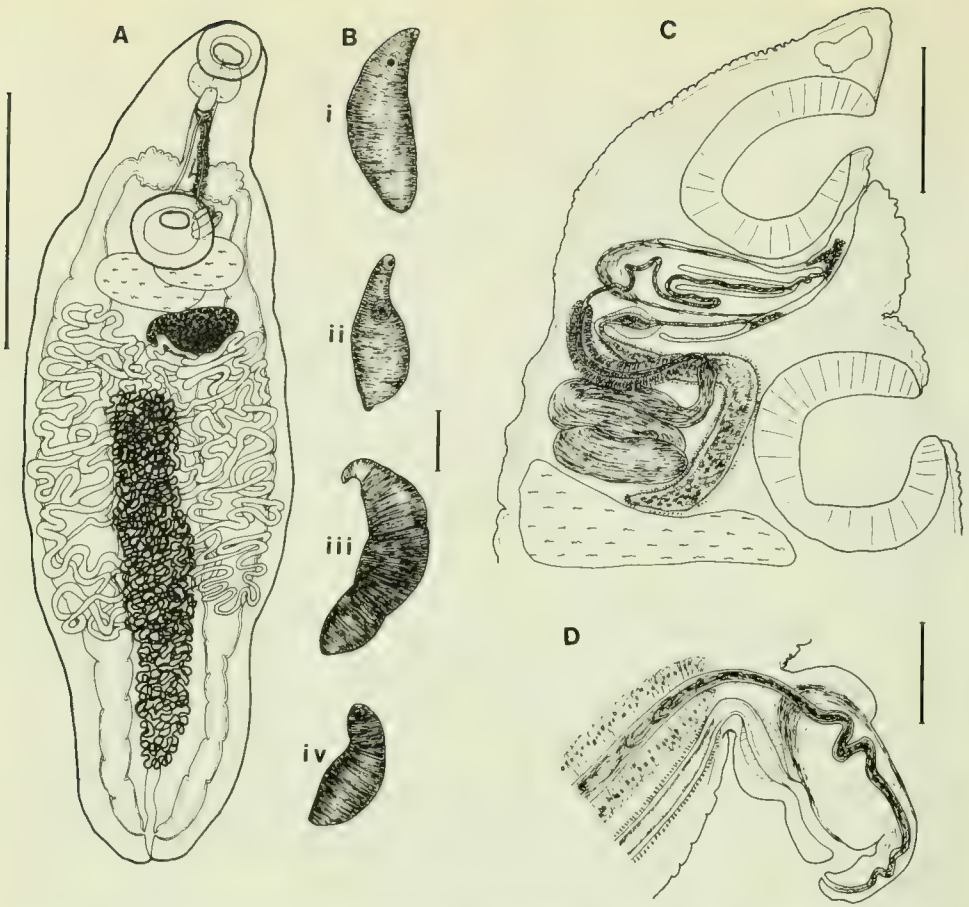

Fig. 12 *Botulus microporus* ex *Alepisaurus ferox*: (A) internal details of worm reconstructed from sections (Iceland); (B) specimens from various localities; (i) off Iceland; (ii) off Madeira (type-specimen); (iii) and (iv) off Miami Beach, Florida; (C) sagittal section of forebody showing terminal genitalia (Miami Beach); (D) sagittal section showing extruded genital atrium (Iceland). Scale: (A, B) 10 mm; (C) 1 mm; (D) 300 μm.

former, which is usually protruded ventrally, leads dorsally or postero-dorsally directly into a large muscular *pharynx*. An oesophagus of variable length, lined with thick, irregular cuticle, leads in an antero-dorsal to posterior direction, depending on contraction, to join the bifurcation of the gut-caeca. The caeca form 'Drüsenmagen' in the 'shoulder'-region, before running into the hindbody, where they dilate considerably and possess greatly folded walls. They are lined with a layer of very long, darkly staining, glandular, villous epithelium. Close to the posterior extremity the caeca are connected to the stem of the excretory vesicle by narrow ducts to form a uroproct (Fig. 12A). The caeca do not appear to fuse medially, as occurs in the larger specimens of *Hirudinella*, for they are separated over much of their length by the vitellarium.

The terminal excretory pore leads into a short, sinuous or sigmoid stem of the *excretory vesicle*. It reaches forward to about the level of the posterior extremity of the vitellarium, where it divides giving off dorsal and ventral arms. These arms are extremely convoluted and very difficult to follow; but they appear to pass dorsally and ventrally within the hindbody. In the forebody,

Table 15 Dimensions of *Botulus microporus* from the present material and from the literature.

Authority	Type-specimens	Guiart (1938)	A. S. Skrjabin (1958)	Stunkard (1965)	Parukhin & Nikolaeva (1967)	Oshmarin (1968)	Present material	
Name used	*Distomum microporum*	*Botulus alepidosauri*	*Profundiella skrjabini*	*Botulus cablei*	*Profundiella alepisauri*	*Mediolecithus pacificus*	*Botulus microporus*	
Host	*Alepisaurus ferox*	*Alepisaurus ferox*	*Alepisaurus aesculapius*	*Alepisaurus borealis*	*Alepisaurus* sp.	*Lamna cornubica*	*Alepisaurus ferox*	
Locality	Madeira	Madeira	Pacific Ocean	Easter Island, South Pacific	Gulf of Mexico	NW Pacific	Miami, Florida	Iceland
Number of specimens	2 of 6 (remainder twisted)	1 of 2	1 of (?)	13	4	1	4 (contracted)	2 (contracted)
Length (mm)	19–25 (20–32)*	27	18·4	11–33·5	23–40	27	11–35	19–31·5
Breadth (mm)	7–9	7	4·0	6·5–12·0	13–15	10	5–11	6–10·5
Forebody (mm)	5–7 extended	–	–	–	–	–	2·3–5	4·2–7
Oral sucker (mm)	1·9–2·3 × 1·7–2·2	–	1·6 diam.	0·9–1·5 diam.	1·35–1·77 × 1·12–2·00	2·22 × 2·34	1·5–2·6 × 1·2–1·7	2–3 × 1·8–2·8
Ventral sucker (mm)	2·3–2·7 × 2·0–2·8	–	1·7 diam.	1·44–2·25 diam.	1·72–2·56 × 1·96–2·66	2·31 × 2·61	1·3–2·5 × 1·3–2·8	2·8–3·1 × 2·5–2·8
Pharynx (mm)	–	–	1·15 × 1·3	–	1·5–1·26 × 1·68	1·62 × 1·98	–	1·5–1·9 × 1·7
Testes (mm)	–	–	2·4 × 1·6	–	2·1–3·08 × 0·84–4·06	1·2 × 3·4 and 1·76 × 2·2	–	–
Ovary (mm)	–	–	1·6 × 1·1	1·0–1·6 × 1·5–1·75	3·3–6·4 × 1·5–2·0	1·6 × 2·2	–	–
Eggs (μm)	35–37 × 26–27	–	36–38 × 23–28	30–34 × 23–25	35–38 × 22–26	30–38 × 19–28	33–36 × 24–28	33–38 × 22–27

* Figures in parentheses from Monticelli (1889).

where they are still extremely convoluted, they appear to pass laterally and unite dorsally or antero-dorsally to the oral sucker. A small number of muscular ducts are also present within the hindbody; but it is not known whether they are branches of the excretory system or some form of lymphatic system.

The two *testes* are usually situated symmetrically to obliquely, with the left usually being slightly antero-dorsally to the right, immediately posterior or postero-dorsal to the ventral sucker. A relatively large, convoluted, tubular seminal vesicle lies dorsally to the ventral sucker. It leads into a tubular pars prostatica, which is surrounded by a delimited layer of gland-cells and lined with anuclear cells. The pars prostatica leads directly or sinuously anteriorly towards the wall of a diffusely muscled '*cirrus-sac*' which surrounds the base of a large, muscular 'cirrus' (Fig. 12C). Just prior to reaching the wall of the 'cirrus-sac', the male duct assumes the form of an ejaculatory duct which passes into the 'cirrus-sac' and opens terminally on the 'cirrus'. The 'cirrus' is peculiar in that it can be invaginated within itself, thus forming a 'cirrus' within a 'cirrus' (Fig. 12C); this is presumably a mechanism associated with the protrusion and storage of a copulatory organ capable of great extension, while requiring only a relatively small 'cirrus-sac' (cf. *Lampritrema*). There is a well-developed genital atrium (Fig. 12C), which is often completely everted (Fig. 12D), and is thus capable of adding length to the 'cirrus'. The genital pore lies mid-ventrally just posterior to the oral sucker.

The *ovary* is transversely oval and lies immediately postero-ventral to the testes, medially or submedially towards the left side of the body. From the postero-dextral margin of the ovary a short oviduct passes, entering a large Mehlis' gland almost immediately. Just within Mehlis' gland it receives the common vitelline duct and Laurer's canal. The muscular Laurer's canal, which may be dilate proximally, winds dorsally to the ovary and opens on the dorsal surface just posteriorly to the testes. The common vitelline duct is fed by a large reservoir lying dorsally to the anterior extremity of the vitellarium. Mehlis' gland extends a short distance along the first part of the uterus, which may be convoluted. Egg and egg-shell formation occur in the next part of the uterus, which we refer to as the uterine oötype*. This region also contains spermatozoa and leads into a broader region of the uterus, the uterine seminal receptacle, which is packed with spermatozoa. The *uterus* then widens further and leaves the region of the ovary, passing posteriorly to a level about two-thirds of the distance from the ventral sucker to the posterior extremity.This region of the uterus is greatly convoluted, lying mainly in the ventral plane, and reaches towards the lateral margins of the body, overlying the caeca. It then passes anteriorly and, as it approaches the level of the ovary, it passes dorsally and begins to develop a thick, muscular wall, forming a metraterm. The metraterm, which is surrounded by gland-cells and lined with a villous epithelium, runs forward either sinuously or directly towards the base of the 'cirrus-sac'. Here it loses its sheath of gland-cells and turns to run, parallel with, but posterior to, the 'cirrus-sac' through a duct, the proximal region of which has a thick, muscular wall (Figs 12C & D). This duct opens into the genital atrium about halfway along the main body of the male organ, but external to the 'cirrus-sac'. When the genital atrium is everted the female pore is protruded through the genital pore with the 'cirrus'. In one of the sectioned specimens spermatozoa could be seen in the genital atrium and inside the metraterm (Fig. 12C). The uterus contains numerous, relatively small, non-filamented eggs. The *vitellarium* consists of many tightly coiled tubules, which fill the ventro-median region of the worm between a level just posteriorly to the ovary and a short distance from the posterior extremity.

Discussion. The two specimens of *Botulus alepidosauri* originally described by Guiart (1938) were in poor condition (they were dried out) and this prohibited a sound description. We have, however, been able to examine specimens of *Botulus* from the type-host, *Alepisaurus ferox*, and this has allowed us to refine the concept of the genus (see Gibson & Bray, in preparation). We have also examined the type-specimens of *Distoma microporum* Monticelli, 1889, which were collected from the type-host (*A.* [=*Plagyodus*] *ferox*) and type-locality (off Madeira) of *B. alepidosauri.*

* In a small sectioned specimen from *A. ferox* off Florida, the proximal region of the uterus contains a tubular, convoluted structure which extends into the uterine seminal receptacle. This may be the detached lining of the female duct from within Mehlis' gland. Distally it can be seen to contain very small eggs which apparently swell to normal size on release. No sign of this structure was found in a larger sectioned specimen.

Although *D. microporum* has been listed as a species of *Hemiurus* by authors such as Looss (1899) and Yamaguti (1971), our examination has convinced us that it is a senior synonym of *B. alepidosauri*.

The genus *Profundiella* was erected for a new species, *P. skrjabini*, from *Alepisaurus aesculapius* (possibly a synonym of *A. ferox*) in the Pacific Ocean by A. S. Skrjabin (1958). There appears to be no significant difference between this genus and *Botulus*, except for the reported presence of a globular seminal vesicle in the former; if true this would be an unusual feature in a 'primitive' hemiuroid (see Gibson & Bray, in preparation). A second species, *P. alepisauri*, was described by Parukhin & Nikolaeva (1967) from *Alepisaurus* sp. in the Gulf of Mexico (*A. ferox* appears be to the only species of the genus recorded in this region); but this species possesses a seminal vesicle which is tubular and coiled. Through the generosity of Dr R. M. Overstreet we have been able to examine specimens of *Botulus* from off Miami Beach, Florida, and these appear to be indistinguishable from *B. microporus*. We agree, therefore, with Stunkard (1965) and Parukhin & Nikolaeva (1974), who consider *Profundiella* a synonym of *Botulus*, and in addition we consider *P. skrjabini* and *P. alepisauri* to be synonyms of *B. microporus*.

In 1965 Stunkard described *B. cablei* from *Alepisaurus borealis* (possibly a synonym of *A. ferox*) near Easter Island in the south-eastern Pacific Ocean. This species appears to be indistinguishable morphologically from *B. microporus*.

In agreement with Parukhin & Nikolaeva (1974), we are of the opinion that *Mediolecithus pacificus* Oshmarin, 1968, known from a single specimen from *Lamna cornubica* in the northwest Pacific Ocean, is also *Botulus* and we consider further that it is probably a specimen of *B. microporus* accidentally swallowed by this piscivorous host.

LAMPRITREMA Yamaguti, 1940

DIAGNOSTIC FEATURES. Body very elongate, slender. Papillae present on surface of forebody. Uroproct absent. Testes in tandem; near middle of hind body. Most of seminal vesicle thin-walled, but distal portion forms thick-walled, muscular 'pars musculosa'. Thick-walled pars prostatica lies ventrally to posterior part of 'cirrus-sac'. Male duct leads into 'cirrus-sac' some distance from its posterior extremity. 'Cirrus-sac' very large, elongate; club-shaped. 'Cirrus' long or short; capable of being extended through genital pore. Genital atrium deep. Ovary near middle of hindbody. Laurer's canal (?) absent. Uterine seminal receptacle (?). Uterus extends back to near posterior limit of vitellarium; mainly coiled intercaecally in post- and pre-ovarian regions of hindbody. Vitellarium a pair of lateral tubules with short, dorsal branches; mainly extra-caecal; passing posteriorly to ovary about halfway to posterior extremity. Parasitic in stomach (occasionally on gills) of marine teleosts (*Lampris* and *Brama*). Immature forms recorded from salmonoids.

TYPE-SPECIES. *Lampritrema miescheri* (Zschokke, 1890) (by monotypy).

Lampritrema miescheri (Zschokke, 1890) Margolis, 1962

Distomum miescheri Zschokke, 1890.*
Lampritrema nipponicum Yamaguti, 1940.
Lampritrema atlanticum Delyamure & Serdyukov, 1970.
Lampritrema hawaiiense Yamaguti, 1970.

TYPE-HOST AND LOCALITY. *Salmo salar*, River Rhine.

RECORDS.

(i) Material studied
(a) From the NE Atlantic
None.

* The appellation *Distomum miescheri*, as pointed out by Margolis (1962), was first used by Zschokke in 1889; but without a description.

(b) From elsewhere

Lampris guttatus [=*regius*] [stomach] Hamazima, Japan (April, 1939), type-material of *L. nipponicum* Yamaguti, 1940. Fragments in transverse serial section. Meguro Parasitological Museum, Tokyo.

(ii) NE Atlantic records from the literature

(a) Mature

None. It is likely that it does occur in this region in *Lampris guttatus* and possibly *Brama rayi* [stomach, oesophagus and (?) possibly gills].

(b) Immature

Salmo salar [oesophagus] River Rhine. Zschokke (1889 : 88; 1890 : 764; 1892 : 831); [stomach] Heitz (1918 : 339; 1919 : 510).

Salmo salar [?] River Elbe. Fritsch (1894 : 110).

Salmo salar [oesophagus] River Tweed, Great Britain. Tosh (1905 : 115).

Aspects of biology. The life-history of this species is not known. Its normal definitive host appears to be the opah *Lampris guttatus* [=*L. regius*, =*L. luna*]; but it also reaches maturity in *Brama rayi* (see Margolis, 1962), although these specimens are smaller. Immature forms are found in salmonoids which, although several of the records are from freshwater, presumably acquire the parasite at sea. It does not appear to be capable of maturing in salmonoids. Records from salmonoids, in addition to those given above, are those from *Oncorhynchus nerka* and *O. gorbuscha* [stomach and gills] in the Sea of Okhotsk and northern Pacific Ocean (Margolis, 1962) and from *Argentina silus* off the eastern coast of Canada (Scott, 1969). The occurrence of the immature form only in salmonoids is surprising unless these records are not entirely accidental as at first suspected. *Lampris guttatus* is essentially piscivorous, and it may be that these teleosts, apparently acting as paratenic hosts, will, in fact, prove to be obligatory.

Previous descriptions. Zschokke (1890 : 781; immature form only); Heitz (1918 : 339; 1919 : pl. 5, fig. 1; immature form only); Yamaguti (1940 : 100; as *L. nipponicum*: 1970 : 119; as *L. hawaiiense*); Margolis (1962 : 942; adult and immature forms as *L. nipponicum*); Scott (1969 : 139; immature form, measurements, only; as *L. nipponicum*); Delyamure & Serdyukov (1970 : 213; as *L. atlanticum*).

Description (Fig. 13). [Taken from Yamaguti, 1940, 1970; Margolis, 1962; Delyamure & Serdyukov, 1970.] Mature specimens of this species have a very long, slender and cylindrical body (Fig. 13A). Measurements for this species are given in Table 16. The short forebody may be arched ventrally and covered by numerous small papillae. The body-surface is otherwise smooth, except for transverse wrinkles possibly caused by contraction during fixation. Yamaguti (1940) notes that the body-wall contains a well-developed layer of longitudinal muscle both in the fore- and hindbodies; but in the hindbody a thick layer of diagonal muscles, which lies within the longitudinal muscle in the forebody, is absent.

The *oral sucker* is ventrally subterminal and surmounted by a pre-oral lobe. The *ventral sucker* is very prominent and significantly larger than the oral sucker (Table 16). The latter leads directly into a large muscular *pharynx*, which in turn leads into a vesicular oesophagus. The gut-caeca possess 'Drüsenmagen' in the 'shoulder'-region and pass back sinuously into the hindbody apparently ending blindly close to the posterior extremity. In the posterior half of the body they develop dorsally-oriented diverticula (Fig. 13E).

The *excretory system* has not been elucidated in detail, as it is very difficult to follow. Judging from the figures of Zschokke (1890), Hertz (1919) and Yamaguti (1970), however, the terminal pore leads into an excretory vesicle with a short stem which divides into dorsal and ventral arms. The arms appear to be very convoluted in both the fore- and hindbodies; but, according to Yamaguti (1940), they do not unite in the forebody. Our examination of his sections, however, suggests otherwise.

The oval *testes* are situated in tandem close to the middle of the hindbody. A tubular, convoluted seminal vesicle lies immediately anteriorly to the ventral sucker, the distal region of which has a muscular wall. It leads into a sinuous or sigmoid, tubular pars prostatica that is surrounded by a dense covering of gland-cells. The elongate, club-shaped '*cirrus-sac*' extends posteriorly

Table 16 Dimensions of *Lampritrema miescheri* from the literature

Authority	Zschokke (1890, 1892)	Tosh (1905)	Heitz (1918)	Margolis (1962)	Scott (1969)
Name used	*Distomum miescheri*	*Distomum miescheri*	*Distomum miescheri*	*Lampritrema nipponicum*	*Lampritrema nipponicum*
Host	*Salmo salar*	*Salmo salar*	*Salmo salar*	*Oncorhynchus* spp.	*Argentina silus*
Locality	River Rhine	River Tweed	River Rhine	Northern Pacific	East coast of Canada
Maturity	Immature	Immature	Immature	Immature	Immature
Length (mm)	10–15	9–17	up to 12	2·7–6·1	6·2–12·9
Breadth (mm)	0·7–0·8	–	–	0·23–0·39	0·46–0·8
Forebody (mm)	2·0–2·5	–	–	–	–
Oral sucker (mm)	–	–	–	0·23–0·32 × 0·22–0·29	0·25–0·36 × 0·30–0·34
Ventral sucker (mm)	–	–	–	0·34–0·46 × 0·25–0·39	0·49–0·63 × 0·34–0·53
Pharynx (mm)	–	–	–	0·13–0·21 × 0·12–0·18	0·18–0·26 × 0·18–0·24
Testes (mm)	–	–	–	up to 0·062 × 0·07	0·02–0·11 × 0·02–0·09
Ovary (mm)	–	–	(?) 1·705*	up to 0·028 × 0·057	up to 0·06 × 0·11
Eggs (μm)	–	–	–	–	–

Authority	Margolis (1962)		Yamaguti (1940)	Yamaguti (1970)	Delyamure & Serdyukov (1970)
Name used	*Lampritrema nipponicum*		*Lampritrema nipponicum*	*Lampritrema hawaiiense*	*Lampritrema atlanticum*
Host	*Brama rayi*		*Lampris regius* (=*L. guttatus*)	*Lampris regius* (=*L. guttattus*)	*Lampris luna* (=*L. guttatus*)
Locality	Gulf of Alaska		Off Japan	Off Hawaii	South Atlantic
Maturity	Immature	Mature	Mature	Mature	Mature
Length (mm)	6·5–10·7	12·3–28·2	30–53	17–70	55·9
Breadth (mm)	0·33–0·47	0·48–1·4	0·9–1·8	0·8–1·6	1·9
Forebody (mm)	–	–	–	*c.* 1/7 length	7·3
Oral sucker (mm)	0·25–0·32 × 0·24–0·29	0·34–0·66 × 0·33–0·54	0·6–0·92 × 0·62–0·9	0·3–0·75 × 0·34–0·76	0·72 × 0·85
Ventral sucker (mm)	0·38–0·53 × 0·26–0·45	0·53–1·06 × 0·53–0·88	1·5–2·25 × 1·1–1·88	0·75–2·0 × 0·7–1·75	1·47 × 1·35
Pharynx (mm)	0·18–0·26 × 0·16–0·21	0·25–0·41 × 0·24–0·36	0·5–0·6 × 0·47–0·72	0·25–0·45 × 0·2–0·5	0·56 × 0·56
Testes (mm)	0·052–0·24 × 0·041–0·11	0·5–0·73 × 0·31–0·73	0·92–2·0 × 0·65–0·1	0·55–2·2 × 0·25–1·0	1·62–1·35 and 1·72 × 1·16
Ovary (mm)	0·029–0·098 × 0·057–0·105	0·25–0·4 × 0·32–0·62	0·6–1·1 × 0·53–0·83	0·33–1·15 × 0·25–0·8	0·93 × 0·97
Eggs (μm)	–	47–57 × 18–24	45–51 × 18–20	52–58 × 21–28	54 × 21

* According to Margolis (1962) this should be 0·1705 and is probably a measurement of Mehlis' gland.

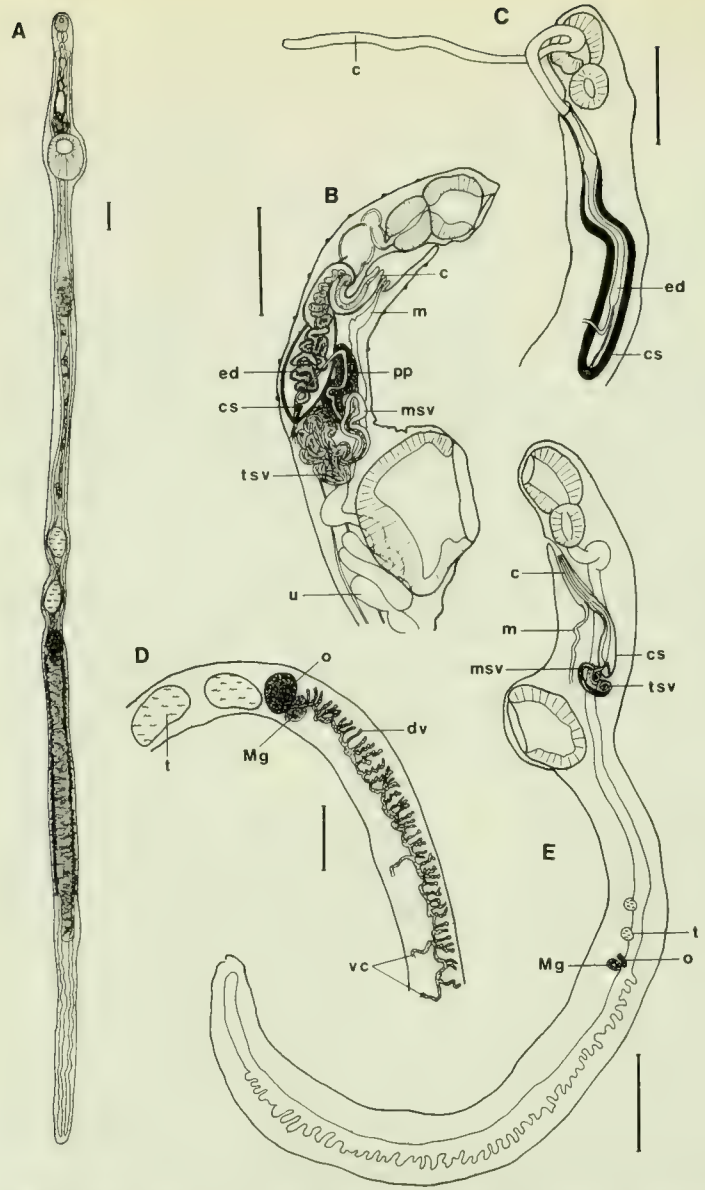

Fig. 13 *Lampritrema meischeri*: (A) mature specimen ex *Lampris guttatus* (modified after Yamaguti, (1940); (B) lateral view of anterior extremity of mature specimen from *L. guttatus* (modified after Yamaguti, 1940); (C) lateral view of anterior extremity of mature specimen ex *L. guttatus* (modified after Margolis, 1962); (D) ventro-lateral view of gonads and one side of vitellarium of mature specimen from *Brama rayi* (modified after Margolis, 1962); (E) lateral view of immature specimen from *Oncorhynchus nerka* [rudimentary vitellarium may be visible in larger specimens] (modified after Margolis, 1962). Scale: (A, B, C) 1 mm; (D, E) 500 μm. [c, 'cirrus'; cs, 'cirrus-sac'; dv, dorsal branches of vitellarium; ed, ejaculatory duct; m, metraterm; Mg, Mehlis' gland; msv, muscular region of seminal vesicle; o, ovary; pp, pars prostatica; t, testis; tsv, thin-walled region of seminal vesicle; u, uterus; vc, vitelline commissures.]

from the base of the genital atrium to the level of the seminal vesicle (Fig. 13B). The pars prostatica passes through the wall of the 'cirrus-sac' subterminally and immediately assumes the form of an ejaculatory duct. This duct is initially narrow, but then becomes broader and more muscular as it passes distally within the 'cirrus-sac', being either straight or convoluted, depending on the extension of the 'cirrus'. The 'cirrus' is a very contractile structure, which may be very short or protruded through the genital pore for a distance of up to 4 mm (Margolis, 1962) (Fig. 13C). The small genital pore lies mid-ventrally to the pharynx.

The globular *ovary* lies just posteriorly to the hinder testis. Mehlis' gland is immediately post-ovarian (Fig. 13D). Although found in other hirudinellids, no Laurer's canal or uterine seminal receptacle have yet been reported. Yamaguti (1940) reports the presence of a minute seminal receptacle within Mehlis' gland; but it is very unlikely that this is a canalicular seminal receptacle and its presence requires confirmation. The *uterus* winds posteriorly from the ovarian complex in the ventral plane, passing the posterior extremity of the vitellarium and overlapping the gut-caeca laterally. It then winds forward between the caeca and dorsally to the descending limb, passing the gonads laterally and becoming the metraterm as it passes into the forebody. The metraterm leads directly or sinuously towards the female pore, which is situated in the genital atrium immediately posterior to the 'cirrus' (Fig. 13B). The oval eggs lack spines or filaments. The vitellarium is tubular and extends laterally between the ovary and the posterior extremity. It appears, essentially, to consist of two main lateral tubules which run posteriorly and give rise to numerous small, dorsally-directed branches (Fig. 13D). According to the literature these small branches are mainly extra-caecal but occasionally unite medially forming commissures. The two main tubules unite in the region of Mehlis' gland, forming a vitelline reservoir.

Immature specimens, from both the final hosts and salmonoids, appear to have a much smaller length to breadth ratio (see Table 18). The gonads and vitellarium may be very reduced or apparently absent in the youngest specimens, but the terminal genitalia and Mehlis' gland are usually quite well developed even at this stage (Fig. 13E).

Discussion. *Distoma miescheri* was described by Zschokke (1890, 1892) and Heitz (1918, 1919) as an immature form from the oesophagus and stomach of *Salmo salar* in fresh water. Further specimens were recorded from this host by Fritsch (1894) and Tosh (1905). The systematic position of this species remained undetermined until the valuable work of Margolis (1962), who recognized it as an immature form of the genus *Lampritrema* Yamaguti, 1940. Margolis found that the description of *D. miescheri* are remarkably similar to immature specimens of *Lampritrema nipponicum* which he had collected from *Oncorhynchus* spp., along with mature and immature specimens from *Lampris guttatus* [=*L. regius*] and *Brama rayi* from the Pacific Ocean. He concluded his study of this problem as follows: 'From the foregoing comparison of the morphology of *D. miescheri* and *L. nipponicum*, and taking into consideration the probable errors in the description of *D. miescheri*, it seems reasonable to conclude that the former species belongs to *Lampritrema*, becoming *L. miescheri* (Zschokke, 1890) nov. comb. Furthermore, it is not unlikely that *L. miescheri* and *L. nipponicum* are identical, but synonymizing these two species must await the discovery and description of adult *L. miescheri* from the Atlantic. If they prove to be synonymous, *L. nipponicum* will have to fall in favor of *L. miescheri*. The occurrence of the same species of *Lampritrema* in the Atlantic and the Pacific Oceans is quite tenable since the two known normal hosts (*Lampris regius* and *Brama rayi*) of *L. nipponicum* in the Pacific have a similarly wide distribution in both oceans.' Since Margolis' work immature specimens of *L. nipponicum* have been recorded from the salmonoid *Argentina silus* in the NW Atlantic by Scott (1969), a new species, *L. atlanticus*, has been described from *Lampris guttatus* [=*L. luna*] in the South Atlantic by Delyamure & Serdyukov (1970), and Yamaguti (1970) has described a new species, *L. hawaiiense*, from *Lampris guttatus* [=*L. regius*] from off Hawaii. Surprisingly, Yamaguti (1971) still maintains that *Distomum miescheri* is unrecognizable, despite the fact that several errors in Zschokke's (1890) description have been explained by Heitz (1918) and Margolis (1962).

L. nipponicum was originally described by Yamaguti (1940) from *L. guttatus* [=*L. regius*] from off Japan and, prior to Margolis' records, had been recorded from the same host off the Californian coast by Arai (1963). The differences between this species and *L. atlanticum* listed by Delyamure & Serdyukov (1970) can all be explained by differences in size and contraction.

Yamaguti (1970) claims that *L. hawaiiense* is a distinct species because of differences in egg-size and the smaller size of the oral sucker and pharynx, when compared with the type-specimens of *L. nipponicum*. These measurements, however, especially that of egg-size, tend to overlap when those of Margolis (1962) and Delyamure & Serdyukov (1970) are included. We are of the opinion, therefore, that, like the related genera *Hirudinella* and *Botulus*, *Lampritrema* is monotypic, and that, as suggested by Margolis (1962), *L. miescheri* is the oldest available name for the type-species.

Family **PTYCHOGONIMIDAE** Dollfus, 1937

DIAGNOSTIC FEATURES. Body medium sized; oval. Body-surface smooth, without spines or plications. Oral and ventral suckers well developed; oral sucker larger than ventral sucker; latter situated in anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus short. Gut-caeca form uroproct. Testes two; post-ovarian; tandem in middle of hindbody. Seminal vesicle dilate, tubular; thin-walled; extending posteriorly into anterior hindbody. Pars prostatica tubular. Ejaculatory duct and hermaphroditic duct short. Permanent sinus-organ a small cone. Sinus-sac absent. Genital atrium contains three distinct concentric folds in its wall which surround sinus-organ. Genital pore mid-ventral in forebody. Ovary oval; pre-testicular in hindbody. Mehlis' gland pre-ovarian. Laurer's canal and uterine seminal receptacle present. Juel's organ and canalicular or blind seminal receptacle absent. Uterine field extends between ventral sucker and a level posterior to testes. Eggs numerous; without filaments. Vitellarium follicular; in lateral fields extending throughout most of hindbody. Excretory vesicle Y-shaped; arms unite twice in forebody. Parasitic in stomach of elasmobranchs (normally carchariniform sharks).

PTYCHOGONIMUS Lühe, 1900

DIAGNOSTIC FEATURES. As family.

TYPE-SPECIES. *Ptychogonimus megastoma* (Rudolphi, 1819) (by monotypy).

Ptychogonimus megastoma (Rudolphi, 1819) Lühe, 1900

Distoma megastomum Rudolphi, 1819.
Distomum soccus Molin, 1858.
Distoma lymphaticum von Linstow, 1903.
Cercaria dentalii Pelseneer, 1906.

TYPE-HOST AND LOCALITY. *Galeorhinus galeus*, Rimini, Adriatic Sea.

RECORDS.

(i) Material studied
(a) From the NE Atlantic
Mustelus mustelus [stomach] Plymouth, Devon, England. BM(NH) Reg. No. 1932.12.6.9. (material of Baylis & Jones, 1933).
(b) From elsewhere
Mustelus mustelus [stomach] Split, Yugoslavia (Sept., 1975). BM(NH) Reg. No. 1976.5.12.5–34.
(ii) NE Atlantic records from the literature
Mustelus mustelus [oesophagus and stomach] Belgium. van Beneden (1871 : 6).
Mustelus mustelus [stomach] Arcachon, Gironde, France. Monticelli (1890 : 426).
Mustelus mustelus [stomach] Plymouth, Devon, England. Nicoll (1914 : 481); Baylis & Jones (1933 : 631); Baylis (1939 : 481).

ASPECTS OF BIOLOGY. Records of intermediate hosts in the NE Atlantic region:
(a) Molluscan host
Antalis vulgaris [= *Dentalium tarentinum*] Wimereux, France. Pelseneer (1906 : 170; as *Cercaria dentalii*).

(b) Crustacean hosts

Atelecyclus sp. [?] Arcachon, Gironde, France. Bouvier, in Dollfus (1937a : 468).

Carcinus maenas [body-cavity] Arcachon, Gironde, France (Nov., 1922). Dollfus (1937a : 461, 468).

Hyas araneus [body-cavity] Luc, Calvados, France. Vaullegeard (1896 : 665).

Maia sp. [body-cavity] Arcachon, Gironde, France. Viallanes, in Monticelli (1890 : 426).

Portunus depurator [body-cavity] Luc, Calvados, France. Vaullegeard (1896 : 665).

Adult specimens of *P. megastoma* occur in the stomach of carchariniform sharks, especially in *Mustelus mustelus* and especially in the Mediterranean region. Outside the northeast Atlantic region this parasite has been recorded from a variety of these sharks. The miracidium enters scaphopod molluscs of the genus *Antalis* [*A. vulgaris* (= *Dentalium tarentinum*) and *A. inaequicostatum* (= *D. alternans*)] and develops, presumably into a mother-sporocyst. Within the daughter-sporocysts almost tailless cercariae develop, but are not released. The daughter-sporocysts, containing the cercariae, leave the scaphopod and fall prey to a wide variety of crabs. Once within the crab, the cercariae penetrate the gut-wall and pass into the body-cavity, where they become unencysted metacercariae. These metacercariae, which may develop progenetically, usually mature when the crab is eaten by a shark (Palombi, 1942b : 117; also information in Palombi, 1941 : 127; 1942a : 1; 1966 : 10). Occasionally immature specimens of *P. megastoma* have been recorded in teleosts (Maclaren, 1903a : 261; Chandra Sekhar & Threlfall, 1970 : 175); but these are presumably accidental infestations, although it is possible that teleosts may serve as transport hosts.

There appears to be no record of this species north of the Belgian coast. This may be connected with the distribution of the first intermediate host in this region, *Antalis vulgaris*, which is not found north of Britain. Other species of *Antalis* occur in more northerly waters, but as yet have not been incriminated.

Previous descriptions. Willemoes-Suhm (1871 : 179); Jacoby (1899 : 16); Jägerskiöld (1900 : 68); von Linstow (1903 : 354); Dollfus (1937a : 459); Yamaguti (1938a : 65; eggs only); Nikolaeva (1966 : 63); de Oliveira Rodrigues *et al.* (1972 : 89).

Description (Figs 14 & 15). This description is based mainly on specimens collected from the stomach of *Mustelus mustelus* from the Adriatic Sea off Split, Yugoslavia. The measurements are given in Table 17. The specimens are relatively large, oval and dorso-ventrally flattened (Fig. 14). The hindbody is slightly broader than the forebody. They have a very prominent, large *oral sucker* and a smaller *ventral sucker* which is situated well inside the anterior half of the body. The body-surface appears smooth, although in fixed specimens it is rugate. Under high magnification, however, it can be seen that the tegument has a villous nature. Acetic acid-fixed specimens are curved dorsally. Specimens fixed under pressure differ considerably from those not flattened: they appear much larger, the ventral sucker tends to be of a slightly different shape, the course of the uterus is much more easily seen and the body-surface is less rugate (Figs 14A & B). For this reason measurements of flattened and unflattened specimens from the present material are given separately in Table 17. It should be noted that prior to fixation all of these specimens were of a similar size.

There is no prepharynx, the oral aperture leading directly into a well-developed *pharynx*. A very short oesophagus passes antero-dorsally from the base of the pharynx. It bifurcates giving rise to two caeca which pass laterally and slightly anteriorly before curving back and leading posteriorly. These broad caeca reach back almost to the posterior extremity of the body, where they narrow considerably and connect directly to the base of the excretory vesicle, very close to the excretory pore, through a very small aperture to form a uroproct.

The *excretory system* is peculiar. The vesicle is Y-shaped, but the stem is very short and narrow, receiving narrow connections from the gut-caeca laterally. The vesicle bifurcates well posteriorly to the posterior limit of the uterus, to form two broad, moniliform arms, which pass laterally dorsal to the caeca and then continue anteriorly dorso-lateral to the caeca. Close to the level of the posterior margin of the oral sucker, the arms bifurcate and re-unite dorsally anterior and posterior to the oral sucker (Fig. 14). Thus the excretory system forms a complete ring around the oral sucker.

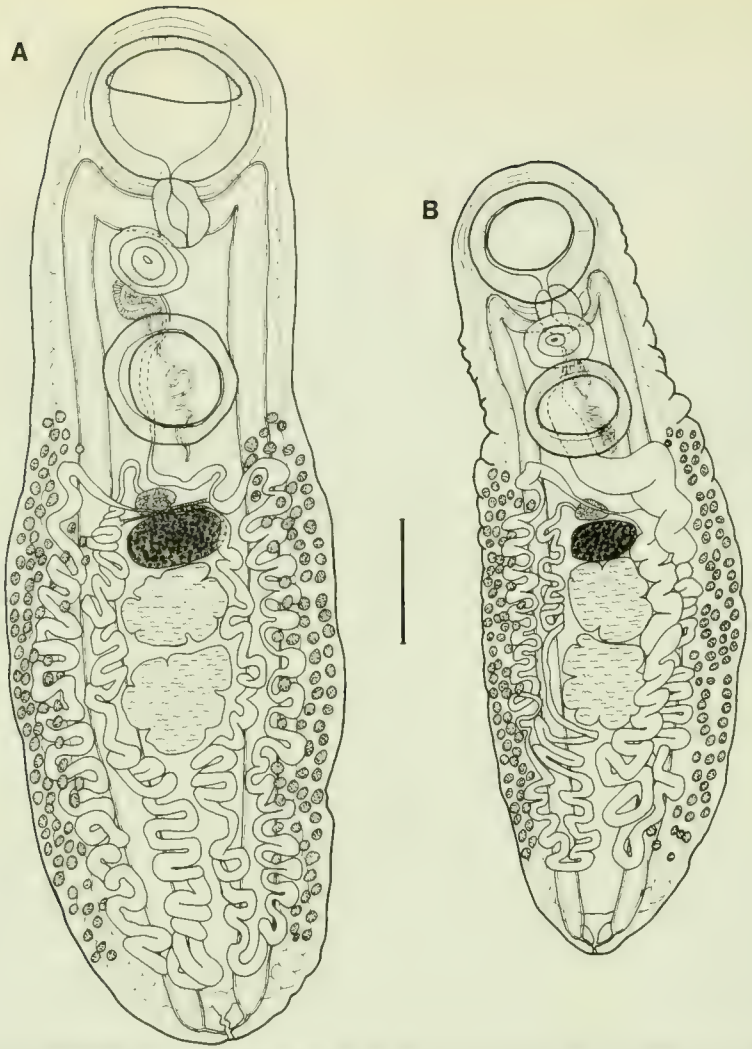

Fig. 14 *Ptychogonimus megastoma* ex *Mustelus mustelus* in Adriatic Sea: (A) specimen fixed under pressure; (B) specimen fixed without pressure. Scale: 1 mm.

The two irregularly-indented, subglobular *testes* occur in tandem close to the middle of the hindbody. A convoluted, tubular seminal vesicle lies dorsally to the ventral sucker; it usually extends from just posterior to just anterior to this sucker. Anteriorly it joins a relatively sinuous or sigmoid pars prostatica. This latter region of the male duct is tubular, although slightly wider in its middle region, surrounded by a dense layer of prostatic cells which are delimited by the surrounding parenchyma, and lined with a layer of cells which project into the lumen (Fig. 15A). There is no prostatic sac. The pars prostatica leads into a very short, oval ejaculatory duct, and this in turn leads into a very short hermaphroditic duct, which occurs within a very small papillate *sinus-organ* (Fig. 15B). The genital atrium is large and its thick wall is convoluted, forming three distinct concentric muscular collars which surround the sinus-organ. The inner collar is the smallest, and the outer collar which is the largest, fills much of the atrium and possesses a terminal glandular

lip which tends to curve over and overlap the inner collars. There is no sinus-sac; but the diffuse musculature of the collars forms a distinct region which extends across the base of the genital atrium. The small genital pore is situated in the middle of the forebody postero-ventrally to the pharynx.

The transversely oval *ovary* is immediately pre-testicular in the anterior region of the hindbody. Closely anterior and slightly dextral to the ovary lies a well-developed Mehlis' gland. Dorsally to Mehlis' gland a relatively short, glandular Laurer's canal opens to the exterior. No canalicular or blind seminal receptacle is present (see Gibson & Bray, in preparation), but a uterine seminal receptacle does occur. The proximal part of the uterus prior to the uterine seminal receptacle apparently acts as an oötype, as the eggs do not appear to form within the region of the ovo-vitelline canal surrounded by Mehlis' gland. The *uterus* winds back to the right of the gonads to within a short distance from the posterior extremity of the body. It then winds anteriorly lateral to the descending region, reaching to the level of Mehlis' gland, where it crosses the body ventrally

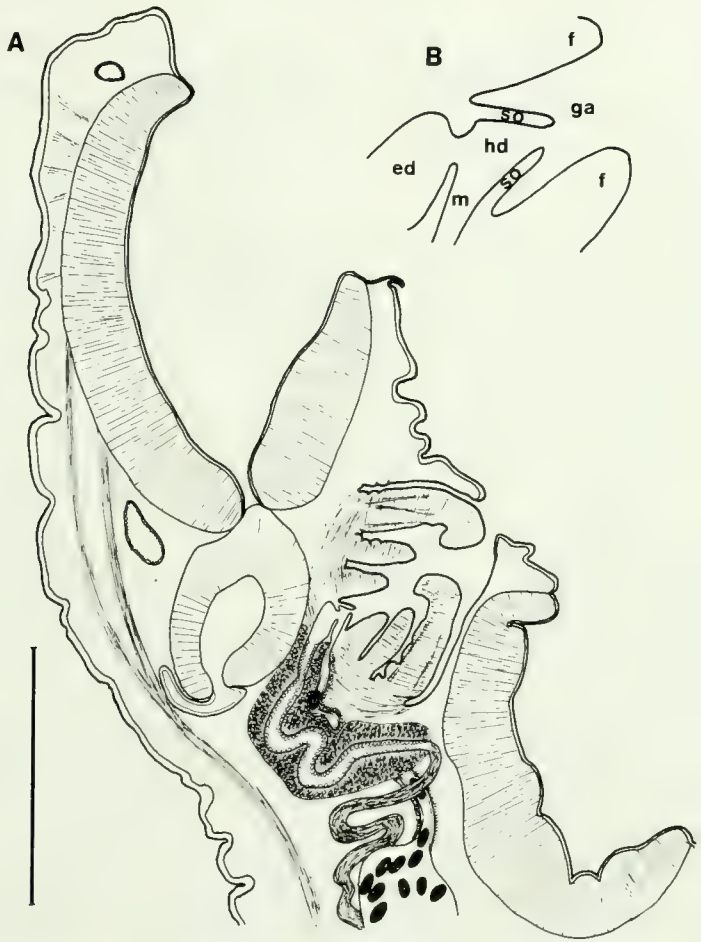

Fig. 15 Terminal genitalia of *Ptychogonimus megastoma*: (A) sagittal section of forebody; (B) enlarged view of region of sinus-organ. [ed, ejaculatory duct; f, first (inner) fold of wall of genital atrium; ga, genital atrium; hd, hermaphroditic duct; m, metraterm; so, sinus-organ.] Scale: (A) 500 μm.

Table 17 Dimensions of *Ptychogonimus megastoma* from the present material and from the literature.

Authority	Jacoby (1899)	von Linstow (1903)	Dollfus (1937)	Nikolaeva (1966)	de Oliveira Rodrigues *et al.* (1972)	Present material	
Host	*Mustelus mustelus* *Galeorhinus galeus*	*Mustelus mustelus*	*Mustelus mustelus*	*Squalus acanthias*	*Mustelus mustelus*	*Mustelus mustelus*	
Locality	Mediterranean and Adriatic Seas	?	Coast of Mauritania	Adriatic Sea	Atlantic coast of North Africa	Adriatic Sea	
Number of specimens	?	?	?	?	?	Flattened 5	Unflattened 3
Length (mm)	10–12 (immat. 4–5)	2·1–2·7	6–8·5	1·5–4·62	3·04–6·34	7·5–8·3	6·0–6·3
Breadth (mm)	3–4 (immat. 1–1·5)	1·1–1·2	2·5–3·5	0·58–1·63	0·66–1·98	2·4–2·7	1·96–2·06
Forebody (mm)	–	–	–	–	–	2·2–2·5	1·62–1·64
Oral sucker (mm)	1·5 diam.	0·63	–	0·41–1·05 × 0·42–0·94	0·77–1·2 diam.	1·0–1·2 × 1·22–1·4	0·98–1·08 × 1·00–1·2
Ventral sucker (mm)	1·2 × 1·37	0·55	–	0·33–0·84 × 0·33–0·75	0·48–0·94 diam.	1·0–1·12 × 0·98–1·12	0·76–0·8 × 0·84–0·92
Pharynx (mm)	–	–	–	0·23–0·46 × 0·19–0·48	0·27–0·58 × 0·33–0·58	0·5–0·55 × 0·45–0·5	0·4–0·47 × 0·38–0·45
Genital atrium (mm)	–	–	–	–	0·3–0·78 diam.	0·5–0·58 × 0·63–0·7	0·3–0·45 × 0·5–0·56
Testes (mm)	0·63–0·93 × 0·7–0·73	–	–	0·16–0·52 × 0·10–0·34	0·52–0·72 × 0·48–0·72	0·5–0·82 × 0·75–0·95	0·45–0·7 × 0·56–0·75
Ovary (mm)	0·41 × 0·77	–	–	0·14–0·43 × 0·08–0·28	0·36–0·56 × 0·24–0·52	0·4–0·48 × 0·75–0·8	0·26–0·35 × 0·53 × 0·56
Eggs (μm)	57 × 34	73 × 44	62–67 × 36–38	47–71 × 25–34	52–72 × 32–40	52–62 × *c.* 28–32 (collapsed)	56–62 × *c.* 30

and winds posteriorly again to the left of the gonads (Fig. 14). Just short of the posterior extremity it again loops forward laterally, forming an ascending limb on the left side, and then passes medially just posteriorly to the ventral sucker. Dorsally to the ventral sucker, where it is often very dilate, the uterus usually narrows suddenly, forming a metraterm which is surrounded by small gland-cells. This relatively long metraterm leads directly towards the terminal genitalia, where it unites with the ejaculatory duct to form a very short hermaphroditic duct (Fig. 15A & B). The numerous eggs lack filaments or spines. Their shells appear to be soft and untanned in the first descending limb of the uterus. The *vitellarium* is follicular and lies in lateral fields which extend from the posterior margin of the ventral sucker to a region approximately level with the posterior limit of the uterus, i.e. just short of the posterior extremity. The two fields are not confluent. The main collecting ducts unite ventrally to Mehlis' gland, and the common duct joins the oviduct within Mehlis' gland.

Discussion. *Ptychogonimus* resembles the azygiid *Otodistomum* in having a wide range of egg-size, although our Adriatic Sea material has a relatively constant egg-size. Yamaguti (1938a) noted that young and fully-developed eggs showed variation of 42–96 × 27–63 μm, and Willemoes-Suhm (1871) recorded even larger differences, 28 × 21 to 86 × 57.* This emphasizes the need for measuring eggs only from the distal region of the uterus. It seems likely that, as in *Otodistomum*' some variation in the egg-size of *Ptychogonimus* is due to growth of the oötype.

Distomum megacotyle Monticelli, 1893, was briefly described from *Mustelus mustelus* at Wimereux, Artois, France, by Monticelli (1893b : 52). This species is based on a single immature specimen which had previously been figured by Monticelli (1890 : 426, fig. 17) as '*Distoma* (forma giovane)'. It was considered by Palombi (1942b : 149) to be a synonym of *P. megastoma*; but the position of the ventral sucker and the apparent structure of the excretory system suggest that this is somewhat unlikely. Monticelli's figure indicates that *D. megacotyle* might be an immature specimen of *Derogenes* accidentally ingested by the shark.

We have not included the description by Vigueras (1956) amongst our 'previous descriptions', as it differs from other descriptions of *P. megastoma*. Vigueras' specimens, from *Cynias canis* off Cuba, appear to possess an oral sucker smaller than the ventral sucker, a vitellarium which is confluent in the post-testicular region and an almost pre-testicular uterus.

Family **SCLERODISTOMIDAE** Odhner, 1927

Prosogonotrematidae Vigueras, 1940.
Mabiaramidae Teixeira de Freitas & Kohn, 1967.

Diagnostic features. Body usually large; stout or elongate. Body-surface smooth, but may be rugate. Oral and ventral suckers well developed; ventral sucker just posterior to middle of body, in middle of body or well inside anterior half of body. Prepharynx absent. Pharynx well developed. Oesophagus short. Gut-caeca terminate blindly close to posterior extremity. Testes two, symmetrical, in tandem or oblique; pre-ovarian; in forebody, dorsal to ventral sucker or in anterior hindbody. Seminal vesicle tubular; convoluted or winding in forebody. Pars prostatica tubular, occasionally with wide lumen; relatively long; convoluted or not; external gland cells may be delimited. Ejaculatory duct present, uniting with metraterm within sinus-organ forming short hermaphroditic duct. Sinus-sac well developed, weakly developed or absent. Permanent sinus-organ present; usually well developed; conical to cylindrical. Genital atrium well developed; often almost entirely filled by sinus-organ. Genital pore mid-ventral in forebody. Ovary globular to oval; post-testicular; in posterior forebody, dorsal to ventral sucker or in anterior to mid-hindbody. Mehlis' gland usually posterior or postero-lateral, occasionally antero-lateral, to ovary. Laurer's canal present; opens dorsally or into rudimentary Juel's organ (see 'Terminology'). Rudimentary seminal receptacle present or absent. Uterine seminal receptacle present. Uterus mainly in either fore- or hindbody; mainly pre- or post-ovarian. Eggs small, very numerous; non-filamented. Vitellarium four to seven convoluted, tubular branches, which may subdivide; either mainly pre-

* There may be some doubt as to the identity of some of Willemoes-Suhm's specimens, as he recorded them up to 20 mm in length. This is much larger than has been recorded by any other author.

or mainly post-ovarian; either mainly in fore- or hindbody. Excretory vesicle Y-shaped; arms united in forebody. Manter's organ (accessory excretory vesicle) present; single or double; dorsal to stem of excretory vesicle. Parasitic in gut (mainly stomach), occasionally body-cavity, of marine teleosts.

Subfamily **PROSORCHIINAE** Yamaguti, 1934

DIAGNOSTIC FEATURES. Body elongate-oval to very elongate. Ventral sucker normally within anterior half of body, but occasionally in middle. Testes tandem to almost symmetrical; in forebody or dorsal to ventral sucker. Pars prostatica broad; external gland-cells delimited. Sinus-sac absent or very weakly developed. Ovary in hindbody. Laurer's canal long and opening into rudimentary Juel's organ or short and opening to exterior on dorsal surface; may or may not be dilated proximally forming rudimentary seminal receptacle. Uterus mainly post-ovarian in hindbody. Vitellarium two or four branching, or seven, convoluted and filamentous tubules; mainly post-ovarian, in hindbody; reaching near to posterior extremity. Manter's organ single.

Prosorchiopsis Dollfus, 1947

DIAGNOSTIC FEATURES. Laurer's canal short; opening dorsally to exterior; distal region may be slightly dilate and possess glandular wall; no rudimentary seminal receptacle present.

TYPE-SPECIES. *Prosorchiopsis legendrei* Dollfus, 1947 (by original designation and monotypy).

Prosorchiopsis legendrei Dollfus, 1947

Prosorchis (*Prosorchiopsis*) *legendrei* Dollfus, 1947.
(?) *Prosorchiopsis aluterae* Yamaguti, 1970.
(?) *Prosorchiopsis nasonis* Yamaguti, 1970.

TYPE-HOST AND LOCALITY. *Centrolophus niger*, Concarneau, Bay of Biscay.

RECORDS.

(i) Material studied
(a) From the NE Atlantic
None.
(b) From elsewhere
Pachymetopon grande [stomach] Ramsgate, nr Durban, South Africa. Collected by R. van der Elst. BM(NH) Reg. No. 1975.9.16.118.
(ii) NE Atlantic records from the literature
Centrolophus niger [body-cavity] Concarneau, Brittany, France (April, 1946). Dollfus (1947 : 314).

ASPECTS OF BIOLOGY. There appears to be no information available with regard to the life-history of the sclerodistomids; but it is interesting to note that, to date, the prosorchiine species appear to be restricted to stromateoid, acanthuroid and percoid members of the order Perciformes.

PREVIOUS DESCRIPTION. Dollfus (1947 : 314).

DESCRIPTION (Fig. 16). This description is based on four specimens of which three are whole-mounts and one has been serially sectioned. Measurements are given in Table 18. This relatively large worm is elongate and subcylindrical, the forebody being broader than the hindbody (Fig. 16A). The *oral* and *ventral suckers* are large and well developed, the latter being slightly larger than the former and situated well inside the anterior half of the body. The hindbody of these specimens is contracted, being in several places invaginated within itself for a short distance, and thus presenting a 'segmented' appearance. These invaginations (Fig. 16A) resemble the invagination of the ecsoma of hemiurids, but do not appear to have been present in Dollfus' (1947) more extended specimens. In the sectioned specimen the oral sucker is withdrawn deeply into the forebody (Fig. 16B). Surprisingly, the body-surface is not entirely smooth, as much of the surface is covered with minute, pointed projections which tend to occur in rows. Closer study of this surface

Table 18 Dimensions of *Prosorchiopsis legendrei* from the present material and from the literature.

Authority	Dollfus (1947)		Yamaguti (1970)		Present material
Name used	*Prosorchis (Prosorchiopsis) legendrei*		*Prosorchiopsis aluterae*	*Prosorchiopsis nasonis*	*Prosorchiopsis legendrei*
Host	*Centrolophus niger*		*Alutera scripta*	*Naso hexacanthus*	*Pachymetopon grande*
Locality	Off Brittany		Hawaii	Hawaii	South Africa
Number of specimens	12	1 immature	2	9	4
Length (mm)	2·5–9·5	5	5·5–8·5	17–31	11–17·5
Breadth (mm)	1/7–1/10 length	0·27	1·0–1·1	up to 2·5	2·4–3·0
Forebody (mm)	–	1·45	–	1/4 length	3·3–5·6
Oral sucker (mm)	–	0·41 × 0·33 depth	0·32–0·5 × 0·43–0·6	1·0–1·8 diam.	1·4–2·05 × 1·0–2·05
Ventral sucker (mm)	–	0·75 × 0·45 depth	0·6–0·95 × 0·65–0·97	1·8–2·5 diam.	1·9–2·6 × 1·8–2·6
Pharynx (mm)	–	–	0·12–0·18 × 0·13–0·21	0·25–0·4 × 0·34–0·5	0·5–1·1 × 0·3–0·7
Testes (mm)	–	–	0·25–0·38 × 0·18–0·43	0·3–0·7 × 0·18–0·33	0·5–0·9 × 0·4–0·7
Ovary (mm)	–	–	0·2–0·32 × 0·18–0·33	0·27–0·6 × 0·13–0·35	0·7–1·0 × 0·5–0·6
Eggs (μm)	28·5–31 × 17–20	–	25–28 × 16–21	23–28 × 14–19	26–31 × 17–21 (usually 28–30 × 18–20)

in sections and comparison with the related *Prosogonotrema*, indicates that the tegument is missing in the region where these projections occur*.

No prepharynx occurs between the oral sucker and the well-developed, oval *pharynx*. It feeds a short dorsally to postero-dorsally directed oesophagus which joins a short, dilate transverse piece which may be the so-called 'diverticulum' observed by Yamaguti (1934) and Srivastava (1936) in whole-mounts of *Prosorchis* spp. The transverse piece is united on each side with the caeca via stout muscular sphincters (Fig. 16E). There are no 'Drüsenmägen'. The caeca, which are narrow and very diverticulate, pass antero-laterally before reflexing laterally to the oral sucker and passing posteriorly in the dorso-lateral field. They follow a direct or sinuous course, depending on contraction, into the hindbody where they terminate blindly near to the posterior extremity.

The *excretory vesicle* is Y-shaped. The arms divide immediately posteriorly to the ventral sucker and re-unite antero-dorsally to the pharynx. The sectioned specimen has a wide, very diverticulate vesicle, filled with granular material. Also present, lying dorsally to the stem of the excretory vesicle, is a single Manter's organ ('accessory excretory vesicle'). This elongate sac has an irregular wall and extends anteriorly almost to the level of the ovary. It is surrounded by a thin muscle-layer which is particularly evident anteriorly and which suggests that it can be evacuated. Manter's organ opens ventrally into the excretory vesicle very close to the terminal pore through a stout sphincter (Fig. 16D). The terminal pore may be slightly withdrawn within the animal.

Two relatively small, oval to rectangular *testes* lie obliquely to tandem in the posterior half of the forebody (Dollfus', 1947, description indicates that they may extend back to a level dorsally to the ventral sucker). Immediately anteriorly to the testes is a long, tubular seminal vesicle which possesses a thin, muscular wall and winds from side to side. It may occasionally extend between the testes. It leads to a tubular, but very broad, pars prostatica with a thick external layer of delimited gland-cells and a thick villous lining (Fig. 16C). It may be relatively straight or arcuate and gives rise to a narrow ejaculatory duct which passes directly into an elongate conical sinus-organ. Towards the tip of the sinus-organ the ejaculatory duct and the metraterm amalgamate to

* It is likely that this is an artifact caused by fixation, and it probably does not occur in nature, although such a shedding of the tegument has been observed in senile sporocysts (Gibson, 1974). As pointed out by Gibson (1976 : 234, footnote), this phenomenon may explain the apparent presence of spines on the surface of *Hirudinella spinulosa* as described by Yamaguti (1938b).

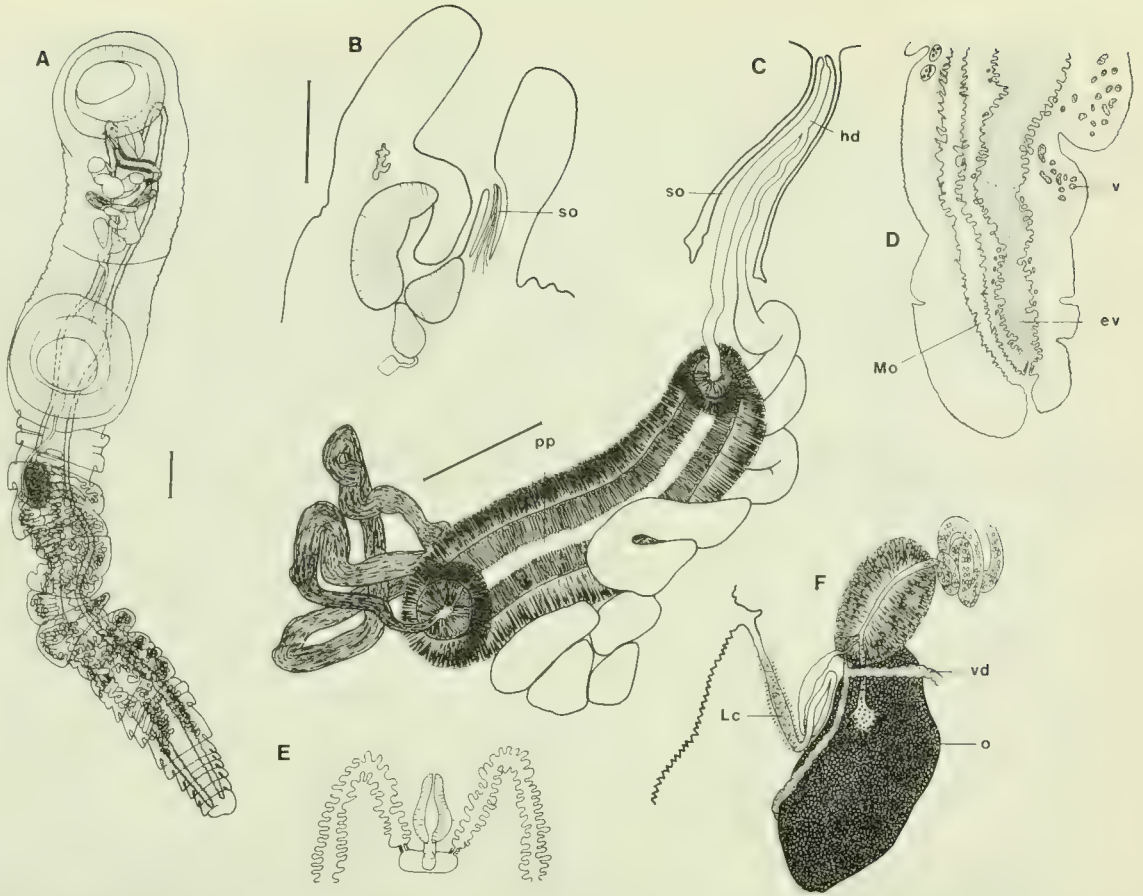

Fig. 16 *Prosorchiopsis legendrei* from *Pachymetopon grande*: (A) whole-mount; (B) anterior extremity of sectioned specimen to show invaginated oral sucker; (C) terminal genitalia; (D) posterior extremity to show stem of excretory vesicle and Manter's organ; (E) anterior region of gut; (F) ovarian complex. Scale: (A, B) 1 mm; (C) 500 μm. [ev, excretory vesicle; hd, hermaphroditic duct; lc, Laurer's canal; mo, Manter's organ; o, ovary; so, sinus-organ; v, vitellarium; vd, vitelline duct.]

form the short hermaphroditic duct. The sinus-organ is probably variable, but in the sectioned specimen it measured 800 μm long and 200 μm at its base. There is no distinct *sinus-sac*. The sinus-organ fills much of the genital atrium, and the genital pore lies mid-ventrally at the level of the pharynx. The arrangement and position of the reproductive organs in the forebody are probably quite variable.

The irregularly oval *ovary* lies submedially a short distance posteriorly to the ventral sucker. It is just dextral and lies in a dorsal plane. Antero-medially it gives rise to an oviduct which passes a short distance into the well-developed Mehlis' gland. Within this gland the oviduct receives Laurer's canal and the common vitelline duct (Fig. 16F). Egg-shell formation occurs within Mehlis' gland. Laurer's canal is short, leads postero-dorsally from Mehlis' gland and opens dorsally at the level of the ovary. It is quite dilate and the distal region contains diffuse material. In the sectioned specimen there is no sign of any type of seminal receptacle, although a uterine seminal receptacle would be expected. The *uterus* loops backwards from the region of Mehlis' gland, gradually widens and continues posteriorly, following a convoluted course, until it reaches a level about a fifth of the length of the hindbody from the posterior extremity. Here it reflexes and retraces its course anteriorly, ventrally to the descending portion, but dorsal or dorso-lateral to Manter's organ. At about the level of the ovary it narrows considerably and continues anteriorly past the ventral sucker either directly or sinuously, depending on the contraction of this region of the body. In the forebody it again expands and follows a winding path before becoming narrower and assuming the form of a short, simple metraterm, which unites with the ejaculatory duct within the sinus-organ (Fig. 16C). The small eggs lack spines or filaments. The *vitellarium* consists of a small number of very long, convoluted tubules which lie ventrally and laterally in the hindbody between the level of the ovary and a level which varies between just anteriorly to the posterior limit of the uterus and the posterior extremity. Whether or not these tubules are branched could not be determined; but they do unite ventro-laterally on either side of the ovary and form single, short, lateral ducts which combine just posteriorly to Mehlis' gland to form a short common duct.

Discussion. There is some disagreement with regard to the validity of the genus *Prosorchiopsis*. It was originally erected as a subgenus of *Prosorchis* by Dollfus (1947) and raised to generic level by Skrjabin & Guschanskaja (1954) because of: (1) the absence of a diverticulum at the junction of the oesophagus and the transverse connection of the gut-caeca; (2) the testes being present dorsal to the ventral sucker instead of entirely within the forebody; and (3) the presence of a short Laurer's canal without a 'distal bulb' and a small proximal 'seminal receptacle'. In our opinion the only valid criterion is the nature of Laurer's canal, as small variations in the position of the testes within the species of this subfamily occur with age and contraction (see Lebedev, 1970 : fig. 7 of *Prosorchis chainanensis*), and because the presence of the oesophageal diverticulum has not been investigated in sectioned material (see above). On this basis we (Gibson & Bray, in preparation) have retained *Prosorchiopsis*. Specimens with a short, tubular Laurer's canal which opens dorsally, we consider to belong to *Prosorchiopsis*, and specimens which have been described as possessing a long Laurer's canal with a proximal swelling (a rudimentary seminal receptacle) and open distally into a terminal 'bulb' (rudimentary Juel's organ*), we consider to be *Prosorchis*. Kurochkin *et al.* (1971) reject *Prosorchiopsis* because '. . . the structure of Laurer's canal at present may be considered for only 3 species (*P. psenopsis*, *P. breviformis* and *P. australis* sp. n.) and such a feature can hardly have taxonomic importance'. This remarkable statement is even more startling when one considers that, of the nine species they accept in *Prosorchis*, six are described in the very same paper. It seems unadvisable to neglect a possibly phylogenetically important taxonomic character because it has not been mentioned in all of the descriptions, some of which are very perfunctory.

The only species of the subfamily Prosorchiinae which can definitely be included in *Prosorchiopsis* are the type-species *P. legendrei* Dollfus, 1947, and *P. aluterae* Yamaguti, 1970. Some of the remaining 13 species which have been described by Yamaguti (1934, 1970), Srivastava (1936), Lebedev

* The nature of Juel's organ, discussed briefly by Gibson & Bray (1975), will be described elsewhere (Gibson & Bray, in preparation) in more detail.

(1970), Bilqees (1971), Kurochkin *et al.* (1971) and Fischthal & Thomas (1972) can definitely be allocated to *Prosorchis*; but in several cases, and especially those described by Kurochkin *et al.* (1971), Laurer's canal has not been mentioned. We suggest that in many of these descriptions the uterine seminal receptacle may have been mistaken for a seminal receptacle. Considering the fact that several workers have described relatively young specimens, that contraction has a considerable influence on body-length and that the eggs of all of these species are of a very similar size, it is likely that future work will show that most of these species of *Prosorchis* are synonymous.

To return to *Prosorchiopsis*, the present material appears to be morphologically very similar to, but larger than, *P. legendrei*. It must be remembered, however, that the latter species is known only from the 12 specimens, several of which were immature, described by Dollfus (1947). It is clear from the specimens of *Prosorchis* and *Prosorchiopsis* so far described that the hindbody of the larger specimens tends to be relatively longer and the gonads relatively smaller than in younger specimens. We have little hesitation, therefore, in considering the present material to be *P. legendrei*, and it is very possible that *P. aluterae* is a synonym. Yamaguti (1970) distinguishes the two species on the grounds that: (1) the testes of *P. aluterae* are within the forebody rather than dorsal to the ventral sucker; (2) Dollfus' figure of the pars prostatica indicates that it is enclosed in a sac (but Dollfus' description makes no mention of this, nor is a sac present in our material; the delimited nature of the external gland-cells of the pars prostatica tend to give this impression in whole-mounts, and this may account for the slightly misleading nature of Dollfus' figure); and (3) Manter's organ is present in *P. aluterae*, but is not mentioned in *P. legendrei*. These characters being rather unconvincing, we have tentatively included *P. aluterae* in the list of synonyms of *P. legendrei*. As it appears to differ from *P. aluterae* only in size (Laurer's canal is not described), we have also tentatively considered *P. nasonis* Yamaguti, 1970, a synonym of *P. legendrei*.

Manter's organ is not normally visible in whole-mounts and, we believe, is probably common to all or most genera within the family Sclerodistomidae. We have seen it as a single structure in *Prosorchiopsis* and *Prosogonotrema* and paired in *Sclerodistomum*, where it is present dorsally or dorso-laterally to the excretory vesicle with which it communicates ventrally and subterminally. Yamaguti (1970) is apparently in error when he states that in *P. aluterae* Manter's organ is 'ventral to the excretory vesicle' and 'communicates with the excretory vesicle dorsally'. It is clear from the distribution of the vitelline tubules (mainly ventral in our specimens) and the uterus (mainly dorsal in our specimens) that some of Yamaguti's transverse sections (see his fig. 217 E) are inverted in relation to the others, and this probably accounts for his remarks.

Family **SYNCOELIIDAE** Looss, 1899

DIAGNOSTIC FEATURES. Body elongate, cylindrical or dorso-ventrally flattened; usually with pedunculate ventral sucker. Body-surface smooth, but commonly papillate on forebody and peduncle. Oral and ventral suckers well developed; may possess accessory suckers around rim. Glandular cells common in subtegumentary parenchyma and within musculature of suckers. Prepharynx absent. Pharynx well developed. Oesophagus short. Cyclocoel usually present, but caeca may end blindly (?) or form uroproct. Testes 11–18 distinct, oval follicles (usually arranged in pairs), 7–8 transverse rows of follicles, or a large number of irregular follicles; pre-ovarian, in hindbody. Seminal vesicle thin-walled, tubular, winding or sinuous; in forebody. Pars prostatica tubular. Ejaculatory duct short. Hermaphroditic duct and genital atrium present, but indistinguishable when sinus-organ is absent. Permanent sinus-organ and sinus-sac present or absent. Genital pore mid-ventral in anterior forebody. Ovary post-testicular; composed of five large, oval and isolated lobes, numerous regular follicles, or (?) a single oval structure. Mehlis' gland post-ovarian. Laurer's canal and uterine seminal receptacle present. Juel's organ and both canalicular and blind seminal receptacles absent, but rudimentary seminal receptacle may be present. Uterus passes posteriorly, but coils mainly in pre-ovarian hindbody. Eggs numerous, small, not filamented. Vitellarium seven (occasionally five or six) isolated, oval lobes, or irregular acinous bunches or rows of follicles; post-ovarian. Excretory vesicle Y-shaped; arms unite in forebody, may initially run in dorsal and ventral fields. Free-floating metacercarial

stage present. Parasitic in branchial and buccal cavities, on skin, in (?) oviduct and in (?) gut of elasmobranchs and marine teleosts.

Subfamily **SYNCOELIINAE** Looss, 1899

DIAGNOSTIC FEATURES. Accessory suckers around rim of suckers absent. Peduncle usually present. Cyclocoel present. Testes 11–18 distinct, oval lobes; usually arranged in pairs. Permanent sinus-organ present or absent. Hermaphroditic duct and genital atrium present, but indistinguishable when sinus-organ is absent. Sinus-sac absent or very rudimentary. Ovary composed of five large, isolated lobes. Rudimentary seminal receptacle may be present as proximal dilation of Laurer's canal. Uterus arranged in large, regular loops dorsally and laterally to gonads. Vitellarium seven (occasionally five or six) small, isolated oval lobes. Parasitic in branchial and buccal cavities (? with occasional records from gut) of sharks and marine teleosts.

*COPIATESTES** Crowcroft, 1948 *sensu nov.*

DIAGNOSTIC FEATURES. Hindbody elongate, tubular. Ventral sucker surmounted on well-developed peduncle. Permanent sinus-organ present. Hermaphroditic duct and genital atrium easily distinguishable. Parasitic in branchial (especially gill-arches and gill-rakers) and buccal cavities (? and intestine) of marine teleosts.

TYPE-SPECIES. *Copiatestes thyrsitae* Crowcroft, 1948 (by original designation and monotypy).

COMMENT. Work which we have carried out for a revision of the Hemiuroidea (Gibson & Bray, in preparation) has indicated that the genus *Syncoelium* Looss, 1899, can be conveniently split into two genera using the presence or absence of a permanent sinus organ as the main criterion. In the forms lacking a sinus-organ, which we have retained in *Syncoelium*, the genital atrium is not distinguishable from the hermaphroditic duct, the hindbody tends to be spatulate rather than tubular, and the ventral sucker is somewhat less pedunclate. Furthermore, these forms have been recorded predominantly from the gills, whereas the forms possessing a sinus-organ generally occur in the buccal cavity and on the gill-arches or gill-rakers. The existing name *Copiatestes* Crowcroft, 1948, is available for the forms with a sinus-organ. The genus apparently consists of the two species; *C. thyrsitae* Crowcroft, 1948, and *C. filiferus* (Leuckart, in Sars, 1885) n. comb. The systematics of this group will be discussed in more detail elsewhere (Gibson & Bray, in preparation).

Copiatestes filiferus (Leuckart, in Sars, 1885) n. comb.

Distomum filiferum Leuckart, in Sars, 1885.
Syncoelium filiferum (Leuckart, in Sars) Odhner, 1911.
Syncoelium katuwo Yamaguti, 1938.
Syncoelium priacanthi Byrd, 1962.

TYPE-HOST AND LOCALITY. *Nematoscelis megalops*, South Atlantic Ocean (region of Tristan da Cunha).

RECORDS.

(i) Material studied
(a) From NE Atlantic
(?) *Trachipterus arcticus* [? buccal or branchial cavity] (?) off Scottish coast.**BM(NH) Reg. No. 1976.5.11.1–2.

* Misprinted '*Capiatestes*' in part of original publication. The name has been corrected by the author in the reprint in the collection of the British Museum (Natural History).

**As the host and locality data for this material were accidentally lost, we are relying on the memory of two people for this information.

(b) From elsewhere

Acantholatris monodactylus [buccal cavity] Off Tristan da Cunha, South Atlantic (36°S, 12°W; Jan., 1926). *Syncoelium filiferum* of Gibson (1976). BM(NH) Reg. No. 1975.3.13.67 85.

Euthynnus alletteratus [intestine] Off Senegal, South Atlantic. *Syncoelium katuwo* of Fischthal & Thomas (1972). U.S.N.M. Coll. No. 71905.

Katsuwonus pelamys [gills] Pacific Ocean (April). Type-material of *Syncoelium katuwo* Yamaguti, 1938. Meguro Parasitological Museum, Tokyo.

Priacanthus boops (? *arenatus*) [gill-rakers] Virginia, U.S.A. (May). Type-specimen of *Syncoelium priacanthi* Byrd, 1962. U.S.N.M. Coll. No. 47300.

(ii) NE Atlantic records from the literature.

None.

Aspects of biology. Nothing is known about the molluscan host of this parasite. Sars (1885) recorded the type-material of this species from the haemocoel of the crustaceans *Nematoscelis megalops* and *Thyssanoessa gregarina* in the South Atlantic (near Tristan da Cunha according to Claugher, 1976). The type-material was re-described by Leuckart (1889) and, in more detail, by Gibson (1976). Re-examination of Sars' original 'Challenger' material by Claugher showed that 90% of the *N. megalops* were infested and that all the specimens of *T. gregarina* were uninfested. The unencysted metacercariae resemble the adults very closely, differing significantly only in the presence of a pair of bladder-like bodies and a pair of long, branched byssal threads which are attached to the posterior extremity (see Gibson, 1976 : 256, fig. 26). A metacercaria of *Syncoelium* sp. has also been recorded from the haemocoel of *Euphausia similis* off Japan by Shimazu (1972). The metacercariae appear to leave the crustacean host and float freely in the sea. Free-floating metacercariae have been recorded by Odhner (1911) from 'south of the Cape', and the metacercariae of *Syncoelium* or *Copiatestes* have been recorded attached externally to the copepod *Candacia pachydactyla* from near the mouth of the river Amazon (Overstreet, 1970) and to a euphausiid from the South Atlantic (Gibson, 1976), and tangled in phenomenal numbers around the feet of seabirds from Chatham Island off New Zealand (Claugher, 1976). The metacercariae presumably use their 'bladder-like bodies' (and possibly the peculiar cells in the parenchyma and suckers) as flotation devices, and the 'byssal threads' act as an aid to attachment to the gills or gill-rakers of the fish host when the free-floating stage is drawn through the buccal and branchial cavities in the respiratory current. It seems that the byssal threads of these metacercariae frequently become entangled in other forms of marine life, and it is possible that the teleost may also acquire this parasite by feeding on marine organisms which have attached metacercariae. The normal habitat of the adult is the buccal cavity or gill-arch of a teleost.

Previous descriptions. Lloyd & Guberlet (1936 : 44); Yamaguti (1938b : 69; as *Syncoelium katuwo*); Byrd (1962 : 136; as *Syncoelium priacanthi*); Lebedev (1968 : 69); Gibson (1976 : 253).

Description (Figs 17 & 18). This description is based on two whole-mounted specimens, one of which was subsequently unmounted and serially sectioned. In both specimens the body forms the shape of an inverted 'Y', with the ventral sucker surmounted on a long peduncle and thrust forward almost like an anterior extension of the hindbody (Fig. 17A). It is likely that, in life, the forebody is directed anteriorly, but curves dorsally and then ventrally, and the peduncle extends ventrally and slightly anteriorly. The configuration of the body is, therefore, somewhat between a '3' and a 'Y' (see Gibson, 1976, and Fig. 17B). These two specimens are rather contracted and, thus, their width measurements exceed that previously recorded (Table 19). The body is cylindrical, the hindbody being stouter than the forebody, especially in its posterior half. Papillae decorate the surface of the forebody, in particular the ventral surface and around the oral and ventral suckers; but the majority of the body-surface is smooth. Both the fore- and hindbodies have transversely folded walls, which appear to be the result of contraction. The body-wall differs in the fore- and hindbodies. In the former there is an outer layer of circular muscle which is split or separated from the outer layer of longitudinal muscle by a vesicular layer of varying thickness. The outer longitudinal layer is separated from a stout inner longitudinal muscle layer by diagonal muscles. In the subtegumentary parenchyma of the forebody, and within the musculature of the oral and ventral suckers, are numerous peculiar, large gland-cells. In the hindbody the vesicular

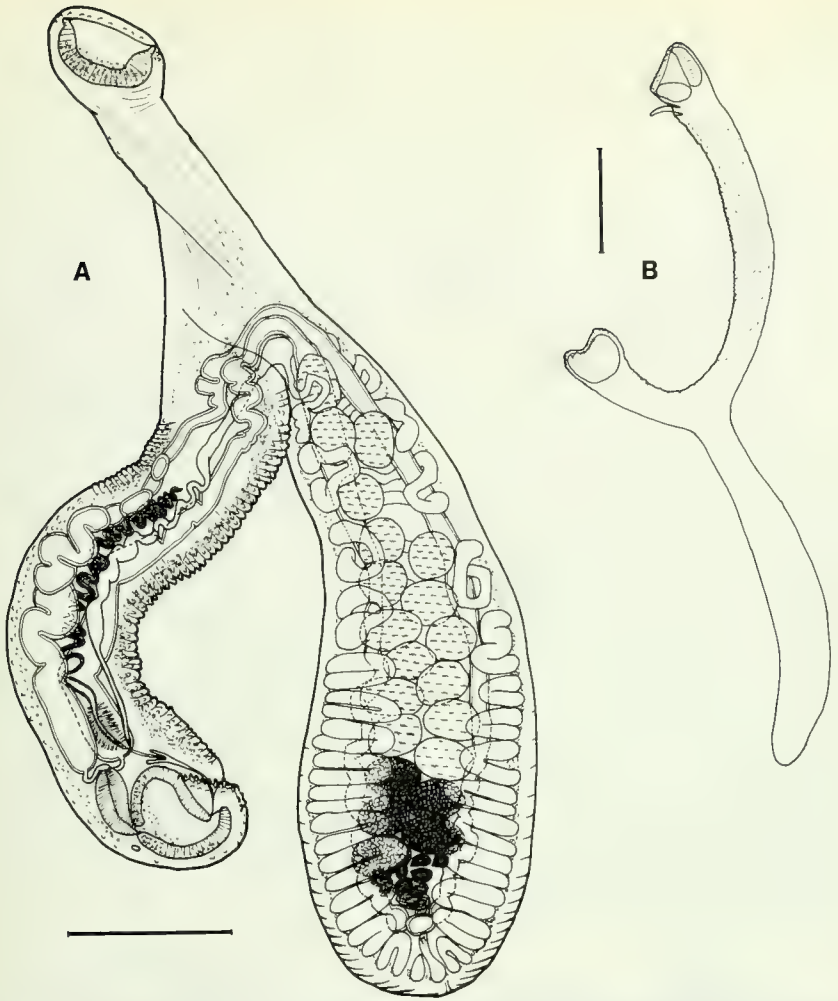

Fig. 17 *Copiatestes filiferus*: (A) ex (?) *Trachipterus arcticus* in North Atlantic; (B) outline, ex *Acantholatris monodactylus* off Tristan da Cunha. Scale: 1 mm.

layer occurs between the inner and outer longitudinal muscle layers and the outer longitudinal and diagonal muscle layers are very reduced. In addition, the large, subtegumentary gland-cells are much less frequent in the hindbody.

The *oral sucker* is well developed and opens subterminally on the ventral surface. The margins are enveloped by folds of the body-wall such that the musculature of the sucker itself does not, apparently, come into direct contact with the substratum. The *ventral sucker*, which lies on a long peduncle, is slightly smaller. Its margins are also covered by outgrowths of the body-wall, leaving a narrow, longitudinal aperture. The forebody is approximately half the total length of the worm.

There is no prepharynx, but a large, well-developed *pharynx* is present. A short, 'cuticular' oesophagus leads dorsally and divides into two lateral ducts of a similar diameter and nature to itself. Dorso-laterally to the posterior margin of the pharynx, the two ducts suddenly enlarge to form dilate gut-caeca, which pass sinuously down the body and unite between the vitellarium and the posterior extremity. There are no 'Drüsenmagen'.

Table 19 Dimensions of *Copiastestes filiferum* from the present material and from the literature.

Authority	Lloyd & Guberlet (1936)	Yamaguti (1938b)	Byrd (1962)	Lebedev (1968)
Name used	*Syncoelium filiferum*	*Syncoelium katuwo*	*Syncoelium priacanthi*	*Syncoelium filiferum*
Host	*Oncorhynchus gorbuscha* *O. nerka*	*Katsuwonus pelamys*	*Priacanthus boops* (? *arenatus*)	*Trachurus declivis* *Thyrsites atun* *Oncorhynchus gorbuscha*
Locality	Puget Sound, Washington State, U.S.A.	Pacific Ocean	Off Virginia, U.S.A.	Off Australia and Primorskiy Kray Territory, U.S.S.R.
Number of specimens	Many	?	1	Many
Length (mm)	5–nearly 10	8·9–10·7	11·96	4·85–9·8
Breadth (mm)	0·5	0·75	0·95	0·58–0·76
Forebody (mm)	–	4·3–5·0	–	–
Peduncle (mm)	–	less than half forebody	slightly less than one-third of forebody	–
Oral sucker (mm)	–	0·48–0·55 × 0·44–0·5	0·56–0·48	0·495–0·67
Ventral sucker (mm)	–	0·52–0·58 diam.	0·73 × 0·34	0·483–0·71 · 0·33–0·71
Pharynx (mm)	–	0·25–0·3 · 0·2–0·24	0·35 × 0·26	0·231 · 0·46 · 0·187 × 0·32
No. of testes	18 (one with 16)	18	15	usually 18 occasionally 16 or 17
Testes (mm)	–	–	0·3–0·39 × 0·42–0·5	0·077–0·32
Ovary (mm)	–	–	–	0·066–0·32
Eggs (μm)	40–50 × *c.* 30	36–42 × 24–27	malformed*	40–51 × 23–39

Authority	Fischthal & Thomas (1972)	Gibson (1976)	Present material
Name used	*Syncoelium katuwo*	*Syncoelium filiferum*	*Copiastestes filiferum*
Host	*Euthynnus alletteratus*	*Acantholatris monodactylus*	(?) *Trachipterus arcticus*
Locality	Off Senegal, West Africa	Off Tristan da Cunha, South Atlantic	(?) Off Scotland
Number of specimens	4	Many	2
Length (mm)	–	5·2–7·2	8·0–8·5
Breadth (mm)	–	0·32–0·5	1·4–1·5
Forebody (mm)	–	–	3·75–4·7
Peduncle (mm)	–	0·8–1·2	1·8
Oral sucker (mm)	–	0·4–0·52 × 0·45–0·6	0·65–0·7 × 0·5–0·6
Ventral sucker (mm)	–	0·4–0·5 × 0·3–0·38	0·58–0·6 × 0·34–0·4
Pharynx (mm)	–	0·25–0·32 × 0·2–0·25	0·45 × 0·28–0·31
No. of testes	17–18	18	16 and 18
Testes (mm)	–	0·12–0·21 diam.	0·25–0·35 × 0·25–0·4
Ovary (mm)	–	–	0·22–0·3 × 0·35–0·45
Eggs (μm)	33–41 × 24–27	35–44 × 18–27	34–40 × 20–28

* Byrd gives them as 14·4–19·2 × 10–14·4.

The tubular *excretory system* is 'Y'-shaped. It has a short, sinuous stem which divides into two sinuous arms dorsally to, and at the level of, the posterior union of the gut-caeca. Initially one arm is in the dorsal and the other in the ventral plane, but the ventral arm soon passes dorsally. They then both extend forward in the dorso-lateral region of the hindbody, enveloped by the uterine loops. At the level of the peduncle the arms pass ventrally and deep into the peduncle, before reflexing and running forward ventro-laterally in the forebody and re-uniting dorsally to the pharynx.

There are 16 and 18 oval *testes* in the two specimens. These are arranged in irregular pairs along the anterior two-thirds of the hindbody. A tubular seminal vesicle extends sinuously, tapering gently, from just anterior to the base of the peduncle, medially between the caeca, to a level about 0·5 mm posteriorly to the pharynx. The distal region is very narrow and has a more muscular wall than the remainder of the seminal vesicle. It leads into the pars prostatica through a stout sphincter. The tubular pars prostatica is broader than the distal region of the seminal vesicle and has a wider lumen. It extends forward, curving antero-ventrally, to about the level of the posterior margin of the pharynx. It gradually tapers anteriorly and only the less muscular anterior half is surrounded by external gland-cells (Fig. 18A). The distal extremity of the pars prostatica might be termed an ejaculatory duct, as it also lacks external gland-cells, but a lining of villous cells is present. This region is linked to the hermaphroditic duct by a sphincter. This latter duct is relatively long, passes antero-ventrally, enters a tubular sinus-organ and opens at its terminus. The sinus-organ lies in a deep genital atrium, which opens mid-ventrally close to the posterior margin of the ventral sucker. In other material the sinus-organ is commonly found protruding through the genital pore. Although the sinus-organ and the region surrounding its base are filled with a diffuse musculature, there is no distinct *sinus-sac*.

The *ovary* consists of 5 isolated, oval lobes, which lie immediately posteriorly to the testes inside the posterior third of the hindbody. Ducts from the ovarian lobes unite to form a long, sinuous oviduct leading posteriorly into Mehlis' gland, which is distinctly delimited from the surrounding parenchyma. As it enters Mehlis' gland, the oviduct receives Laurer's canal and the common vitelline duct (Fig. 18B). Laurer's canal is dilate proximally, forming a rudimentary seminal receptacle containing degraded seminal and vitelline material. Surrounded for much of its length by gland cells, it passes dorsally towards the left side of the body at the level of Mehlis' gland. The female duct continues through Mehlis' gland, but not as an oötype as the ova and vitelline cells pass independently through the uterine seminal receptacle, which winds posteriorly to the level of the inter-caecal union. The *uterus* continues to the posterior extremity, before passing forward through a series of large, regular loops which envelope the gonads dorsally and laterally. Posteriorly,

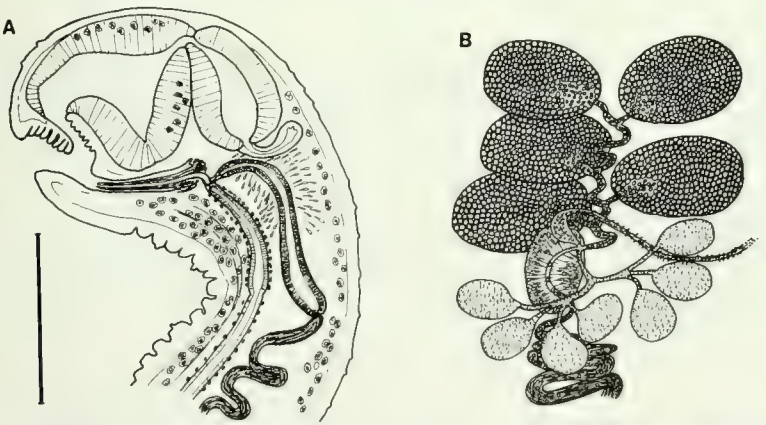

Fig. 18 *Copiatestes filiferus* ex (?) *Trachipterus arcticus*: (A) sagittal view of anterior forebody; (B) diagrammatic ventro-lateral view of ovarian complex. Scale: (A) 500 μm.

the uterus is wide and contains isolated ova and vitelline cells. More anteriorly these cells become grouped together and enclosed in thin, membranous shells, and the vitelline cells appear to subdivide. At about the middle of the hindbody, the uterus narrows, its wall becomes thick and glandular and, at the same time, the egg-shells become thicker, tanned and harder. The uterus passes forward mid-ventrally in the forebody following a sinuous course, and gradually assumes the form of a metraterm (i.e. the wall becomes thicker and more villous) at about the level of the distal extremity of the seminal vesicle. Anteriorly, there is a sphincter at the junction between the metraterm and the hermaphroditic duct. Fully-formed eggs are present in one specimen only; in the sectioned specimen the uterus contains small, deformed eggs and globules of shell-material. The *vitellarium* is composed of seven small, isolated and oval to tear-shaped lobes situated between Mehlis' gland and the posterior union of the caeca.

Discussion. The two specimens collected from the NE Atlantic region differ from the descriptions of *C. filiferus* in the literature in both size and shape. The difference in body-shape can probably be explained by the fact that the specimens were fixed *in situ*, and, if the fish had not been immediately preserved or if the preservative penetrated the branchial or buccal region slowly, then this configuration might have occurred as the animal, attached by its ventral sucker, attempted to escape. A relatively slow fixation is also consistent with the contracted condition of the specimens. The bulk of these specimens is, however, the major difference, the hindbody being at least twice as broad as previously described in specimens of similar length (Table 19). It seems likely that, in its extended form, these specimens fall within the range of *C. thyrsitae* Crowcroft, 1948. They differ from this species in egg-size, 34 40 × 20 28 μm, as opposed to 25 33 × 15 21·5 μm (Crowcroft, 1948; Manter, 1954; Lebedev, 1968). Their egg-size fits reasonably well into that of *C. filiferus* (Table 19). There being no significant morphological differences, and taking into account the limitations in our knowledge of the effects of host or season on size, we have for the present retained these specimens in our conception of *C. filiferus*.

The present material appears to represent the first record of *Copiatestes* in the northern north Atlantic, apart from a single specimen recorded by Byrd (1962) as a new species, *Syncoelium priacanthi*, from the gill-rakers of *Priacanthus boops** 80 km (50 miles) off the coast of Virginia. This location, incidentally, appears to be far north of the normal range of this fish, which normally occurs in the South Atlantic, especially in the region of St Helena, and in the Indo-Pacific region. We have examined the type- and only specimen of this species and consider it identical with the present material, except that it is in an extended condition. Byrd (1962) gives egg-measurements of 14·4 19·2 × 10–14·4 μm, which is much smaller than that recorded for *C. filiferus*. Our examination of the type-specimen, however, revealed that the eggs are malformed, as in one of the specimens from *T. arcticus*. We, therefore, consider *S. priacanthi* a synonym of *C. filiferus*. It is interesting to note that two of the three specimens recorded from the northern north Atlantic have malformed eggs.

C. filiferus appears to be most common in the South Atlantic, in southern Australasian waters and in the northern Pacific Ocean. As *Trachipterus arcticus* is believed to occur only in the north-east Atlantic and Mediterranean Sea (Palmer, 1961), it must be assumed that the parasite was acquired in this region. The range of *Nematoscelis megalops*, which appears to be the most important known intermediate host of this parasite in the South Atlantic (Claugher, 1976), does extend north into this region (Einarsson, 1945; Mauchline & Fisher, 1969; Gopalakrishnan, 1974). This same euphausiid also occurs in the southern Australasian region, but not in the north Pacific, although other species of the genus do. The great concentrations of metacercariae in certain regions, such as Tristan da Cunha and Chatham Island, suggests that the distribution of *Copiatestes* spp. may be somewhat limited by the distribution of suitable molluscan hosts and that the latter occur on the continental shelf.

* The host given on the label with the specimen we examined is *Priacanthus arenatus*. This species occurs relatively commonly in the Gulf of Mexico and its range extends from the Brazilian coast to the region of Rhode Island.

Addendum to 'primitive' Hemiuroidea

Distoma gigas Nardo, 1827

Hirudinella gigas (Nardo) Örley, in Blanchard, 1891.

TYPE-HOST AND LOCALITY. *Luvarus imperialis*, Venice, Adriatic Sea.

RECORDS.

(i) Material studied

None.

(ii) NE Atlantic records from the literature

Luvarus imperialis [stomach] British Coast. Örley (1881, unpublished M.S. in library of British Museum (Natural History)); Monticelli (1889 : 322); Blanchard (1891b : 480). These refer to a single specimen from the collection of the British Museum (Natural History) which appears to have been lost prior to a reorganization of the collection carried out in 1914.

ASPECTS OF BIOLOGY. This parasite is exclusive to *L. imperialis* and has been recorded on four other occasions (Nardo, 1827; Monticelli, 1893a; Setti, 1894; Parona, 1902), all from the Mediterranean Sea in the region of Italy. No information on the life-history is available and all we know of its biology is its location in the stomach (Monticelli, 1893a, recorded it from the intestine) of the louvar. This is a large, rare, deep-water fish which feeds mainly on gelatinous zooplankton. *Distoma gigas* has, on two occasions, been found infesting the same fish as the accacoeliid *Tetrochetus raynerii* (Nardo, 1833), which appears to be the only other known trematode-parasite of the louvar.

PREVIOUS DESCRIPTIONS. Nardo (1827 : 68; 1833 : 523); Monticelli (1889 : 322; 1893a : 171); Blanchard (1891b : 480); Setti (1894 : 1). Only Setti describes any internal features.

DESCRIPTION. (Fig. 19) The following is based almost entirely on the work of Setti (1894), who prepared sections apparently from a single specimen. Measurements from the literature are given in Table 20.

Table 20 Dimensions of *Distoma gigas* Nardo, 1827, from *Luvaris imperialis* taken from the literature.

Authority	Nardo (1827, 1833)	Monticelli (1889)	Blanchard (1891b)	Monticelli (1893a)	Setti (1894)
Locality	Gulf of Venice		British coast	Palermo	Gulf of Genoa
Number of specimens	2		1	2	1
Length (mm)	135	(*c.* 75)	70–80	80	120
Breadth (mm)	7–12	(*c.* 7)	7–8	–	*c.* 10 (*c.* 16)
Forebody (mm)	–	(*c.* 6)	(*c.* 5)	–	*c.* 20 (*c.* 19)
Oral sucker (mm)	–	(*c.* 1·5) diam.	–	–	aperture *c.* 2 (*c.* 3)
Ventral sucker (mm)	–	(*c.* 5) diam.	(*c.* 5) diam.	–	aperture *c.* 8 (*c.* 10)
Testes (mm)	–	–	–	–	1·5 diam. in T.S.
Eggs (μm)	–	–	–	–	35 × 20

Measurements in parentheses were calculated from the author's illustration.

The body of this extremely large digenean, which when alive tends to be of a reddish colour, is cylindrical, although it may taper towards its extremities from the widest point of the body at the level of the ventral sucker (Fig. 19A, B & C). The forebody is short and almost pyramidal.

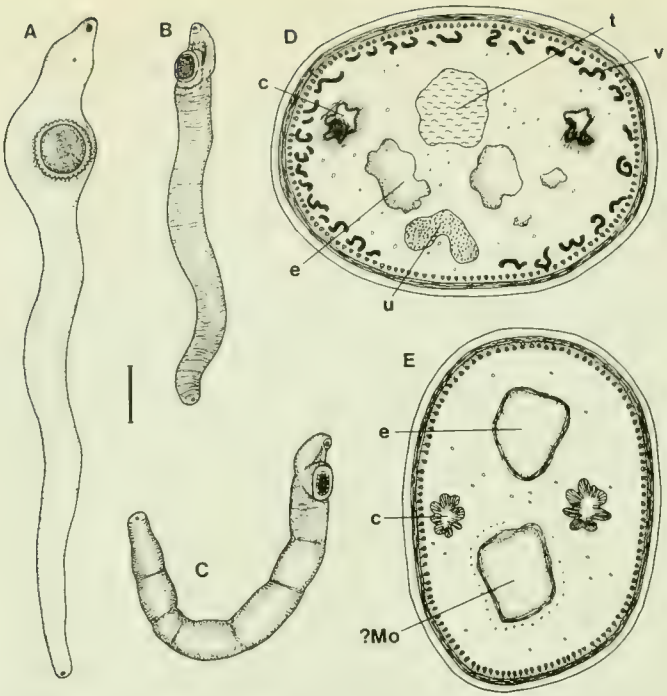

Fig. 19 *Distoma gigas*: ex *Luvarus imperialis*: (A) whole specimen (modified after Setti, 1894); (B) specimen from B.M. collection (modified after Blanchard, 1891b); (C) specimen from B.M. collection (modified after Monticelli, 1889); (D) transverse section at the level of the gonads (modified after Setti, 1894); (E) transverse section at the level of the last fifth of the body (modified after Setti, 1894). Scale: (A, B, C) 10 mm. [c, gut-caecum; e, excretory vesicle; ?mo, possibly Manter's organ; t, testis; u, uterus; v, vitellarium.]

Although fixed forms tend to exhibit transverse rugations, the body-surface can be considered smooth, as these are probably produced by contraction. The large *ventral sucker* is about four times as large as the *oral sucker*, which opens subterminally. The former possesses a marginal, fluted flange, which is apparently external in live specimens and lies within the margin of the ventral sucker in fixed material. This feature has been noticed by all of the authors who have described this species. The terminal excretory pore is also very evident superficially.

The body-wall has a thick tegument beneath which lies a thick layer of circular muscle. On the inner side of this layer there are two layers of longitudinal muscle. The outer contains small muscle-bundles and the inner large bundles. These two layers tend to be somewhat interspersed, the outer longitudinal muscle-bundles lying between those of the much larger inner longitudinal muscle-bundles (Fig. 19E).

There are no data concerning the prepharynx and *pharynx*, but there is apparently a short oesophagus which gives rise to two narrow caeca. These pass posteriorly, following a sinuous course, to end blindly close to the posterior extremity. The caeca possess, over at least some of their length, a lining of extremely long villi, which measure 250–300 × 12–14 μm and extend deep into the lumen (Fig. 19E). In other regions (Fig. 19D) the lumen contains a brown substance (possibly the residue of semi-digested blood).

The terminal *excretory pore*, according to Setti, leads into a short stem, which divides into two stout anteriorly directed arms. According to his figure (see Fig. 19E) the arrangement of the gut indicates that these arms are initially in the dorsal and ventral planes, but are lateral at the level

of the gonads (Fig. 19D). The remainder of the system is not known, but it is possible that the system possesses secondary branches. Setti reports that one of the arms is surrounded by a ring of small longitudinal muscle-bundles (Fig. 19E) and is, therefore, reminiscent of Manter's organ in *Prosorchiopsis legendrei* (see above). These bundles are not shown in the figure at the level of the gonads (Fig. 19D).

Many details of the reproductive system are omitted from Setti's description. The *testes* and *ovary* are close together immediately 'beneath' (? posterior to) the ventral sucker, and appear to be circular in transverse section. It is not clear whether the testes lie anteriorly to the ovary. The *uterus* occupies much of the hindbody, extending posteriorly, and following a convoluted path, to within 20 mm of the posterior extremity (not shown in figure of last fifth of body; Fig. 19E). It measures up to about 300 μm in diameter and contains numerous non-filamented eggs. The *vitellarium* is composed of convoluted tubules, measuring about 115 μm in diameter, and occurs in the hindbody between the ventral sucker and a level about 10 mm from the posterior extremity. It lies in the parenchyma immediately beneath the inner longitudinal muscle-layer (Fig. 19D), and except for a small gap (? dorsally) almost surrounds the body.

Discussion. Only about seven specimens have been recorded, all from *Luvarus imperialis*, and all, apart from the British record, from the Mediterranean Sea. The systematic position is not known. Several early authors compared it (superficially) with *Hirudinella ventricosa* (Pallas) and *Otodistomum veliporum* (Creplin), Cobbold (1867) considered it to be a synonym of *Distoma clavatum* (= *Hirudinella ventricosa*) and Orley (1881, unpublished manuscript, referred to by Blanchard, 1891b) called the specimen, then in the collection of the British Museum (Natural History), *Hirudinella gigas* (Nardo). Juel (1889) suggested that it was a doubtful member of the genus *Apoblema* Dujardin (= *Hemiurus* Rudolphi). Both Lühe (1901) and Looss (1912) indicated that *D. gigas* is not an accacoeliid, but Dollfus (1960) states that it may be related to the 'Accacoelioidea', a group within which he includes the Accacoeliidae and possibly the Hirudinellidae.

The size and the few details of the anatomy that are known indicate that this species is probably a 'primitive' hemiuroid. The only hemiuroid groups which have members approaching the size of this species are the Hirudinellidae and the Azygiidae (*Otodistomum* only). As it lacks a follicular vitellarium *D. gigas* cannot be an azygiid. The distribution of the uterus and vitellarium do not correspond with any known genus of hirudinellid, and the apparent absence of a uroproct distinguishes it from most accacoeliids and hirudinellids. It is conceivable that *D. gigas* represents a new genus of hirudinellid; but a further possibility exists. The small longitudinal muscle bundles around one of the excretory arms resembles closely the situation around Manter's organ in *Prosorchiopsis* (see Figs 16D & 19E). The fact that they are absent from the more anterior section (Fig. 19D), suggests that, if Manter's organ is present, it terminates posteriorly to the level of this section and the main system bifurcates posteriorly to the gonads. It is possible, therefore, that *Distoma gigas* is a sclerodistomid related to the prosorchiines.

Host–parasite list

Class **Chondrichthyes**

Order **Hexanchiformes**

Hexanchus griseus Gmelin: *Otodistomum veliporum* (Creplin).
Chlamydoselachus anguineus Garman: *Otodistomum cestoides* (van Beneden).

Order **Squaliformes**

Centroscymnus coelolepis Bocage & Brito Capello: *Otodistomum cestoides* (van Beneden).
Dalatias licha (Bonnaterre): *Otodistomum veliporum* (Creplin).
Echinorhinus brucus (Bonnaterre): *Otodistomum veliporum* (Creplin).
Etmopterus princeps Collett: *Otodistomum plunketi* Fyfe.
Somniosus microcephalus (Bloch & Schneider): *Otodistomum veliporum* (Creplin).
Squalus acanthias Linnaeus: *Otodistomum veliporum* (Creplin).

Order **Rajiformes**

Raja batis Linnaeus: *Otodistomum cestoides* (van Beneden).
Raja clavata Linnaeus: *Otodistomum cestoides* (van Beneden).
Raja fullonica Linnaeus: *Otodistomum cestoides* (van Beneden).
Raja fyllae Lutken: *Otodistomum* sp. metacercaria.
Raja lintea Fries: *Otodistomum cestoides* (van Beneden).
Raja nidarosiensis Collet: *Otodistomum cestoides* (van Beneden).
Raja radiata Donovan: *Otodistomum cestoides* (van Beneden).
Raja spinicauda Jensen: *Otodistomum cestoides* (van Beneden).

Order **Torpediniformes**

Torpedo marmorata Risso: *Otodistomum veliporum* (Creplin).
Torpedo torpedo (Linnaeus): *Otodistomum veliporum* (Creplin).

Order **Carchariniformes**

Mustelus mustelus (Linnaeus): *Ptychogonimus megastoma* (Rudolphi).

Order **Chimaeriformes**

Chimaera monstrosa Linnaeus: *Otodistomum* sp. metacercaria.

Class **Osteichthyes**

Order **Anguilliformes**

Conger conger (Linnaeus): *Otodistomum* sp. metacercaria.

Order **Salmoniformes**

Alepisaurus ferox Lowe: *Botulus microporus* (Monticelli).
Salmo salar Linnaeus: *Lampritrema miescheri* (Zschokke) immature.

Order **Lophiiformes**

Lophius piscatorius Linnaeus: *Otodistomum* sp. metacercaria.

Order **Gadiformes**

Coelorinchus caelorhinchus (Risso): *Otodistomum* sp. metacercaria.
Molva molva (Linnaeus): *Otodistomum* sp. metacercaria.
Rhinonemus cimbrius (Linnaeus): *Otodistomum* sp. metacercaria.

Order **Lampridiformes**

(?) *Trachipterus arcticus* (Brunnich): *Copiatestes filiferus* (Leuckart, in Sars).

Order **Perciformes**

Centrolophus niger (Gmelin): *Prosorchiopsis legendrei* Dollfus.
Luvarus imperialis Rafinesque: *Distoma gigas* Nardo.
Thunnus alalunga (Bonnaterre): *Hirudinella ventricosa* (Pallas).
Xiphias gladius Linnaeus: *Hirudinella ventricosa* (Pallas).

Order **Pleuronectiformes**

Glyptocephalus cynoglossus (Linnaeus): *Otodistomum* sp. metacercaria.
Hippoglossoides platessoides (Fabricius): *Otodistomum* sp. metacercaria.

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The genus *Urocythereis* (Crustacea : Ostracoda) in Europe, with particular reference to Recent Mediterranean species

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Summary

This study is a detailed taxonomic revision of all the known Recent species of the genus *Urocythereis*. Using appendage and carapace characters, five species are redescribed and three new species (*U. britannica*, *U. colum* and *U. neapolitana*) are introduced. In addition, three fossil species are briefly described and type-specimens proposed for two of them (*U. favosa* and *U. lumbricularis*). Where possible, biostratigraphical and ecological data are given. Shell morphology and the development of ornamentation are discussed. A fossal pattern common to many of the species of *Urocythereis* has been recognized.

Introduction

During the preparation of this paper all the eight known Recent species of *Urocythereis* have been examined. Details of their ecological and stratigraphical distribution are given, and features of the carapace and the soft parts which may be used as reliable specific characters are discussed. It is beyond the scope of this present study to undertake a revision of the fossil forms. Nevertheless, three fossil species, *U. favosa* (Roemer) (the type-species), *U. seminulum* (Seguenza) and *U. lumbricularis* (Terquem) are briefly described and certain stratigraphically important points are considered. In addition, a further one, or possibly two new species from a single sample of beach sand from Libya, N. Africa, are illustrated (Pl. 17), but as few specimens were available and none contained soft-parts, they are for the present left in open nomenclature.

Species of *Urocythereis* have been recorded from the Miocene to Recent. All are large (0·75–1·0 mm) and heavily calcified and are thus readily preserved as fossils. As far as I am aware, the genus occurs only in Europe, although a specimen figured by Sylvester-Bradley & Benson (1971) as 'cf. *Urocythereis*' from S. Africa may be referable to this genus. Living species are usually restricted to coarse sand bottoms at depths of down to 40 m.

In the Mediterranean there are numerous species, both fossil and living, most of which have been inadequately defined. Furthermore, there has been a tendency to 'lump' different forms into single species due to the absence of reliable criteria by which to discriminate individual species within this complexly ornamented group.

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Material examined

During the course of this study, many specimens from the Mediterranean and NW Europe were examined. The principal sources of material were:

(1) G. W. Müller collection: several hundred specimens of *Urocythereis margaritifera* (Müller), one of which was chosen as lectotype, were found in good condition in the Müller collection whilst it was on loan to the Zoological Station, Naples, Italy, during December 1974. The collection is now housed jointly in the Crustacea Division of the Zoological Museum, Berlin, E. Germany, and the Zoological Institute, Greifswald, E. Germany.

(2) G. S. Brady collection, Hancock Museum, Newcastle-upon-Tyne: the type-specimens of *Cythere oblonga* Brady from the Levant were not found nor were they on loan at the time. They must therefore be presumed lost. However, many specimens of *Urocythereis britannica* Athersuch sp. nov. were found in good condition.

(3) Remane collection, Zoological Museum, Hamburg: specimens of *Urocythereis* '*oblonga*' were made available by Professor G. Hartmann.

(4) The Recent ostracod collection of the British Museum (Natural History) was searched thoroughly and many specimens of *Urocythereis* spp. from Britain and the Mediterranean were examined.

(5) I am most grateful to Professor G. Ruggieri, Dr G. Bonaduce and Dr J. E. Whittaker for allowing me to examine their private collections.

(6) Material from the Terquem collection containing *U. lumbricularis* (Terquem) from the Pliocene of Rhodes was obtained by Professor P. C. Sylvester-Bradley from the Museum of Natural History, Paris.

(7) Over 250 samples from Cyprus were collected by me during autumn 1973 from depths of 0–40 m off the coasts of Cyprus. Three species of *Urocythereis* were identified, two of which are 'new' and described herein.

Carapace morphology of *Urocythereis*

The terminology used in the description of the surface features of the carapaces follows Sylvester-Bradley and Benson (1971).

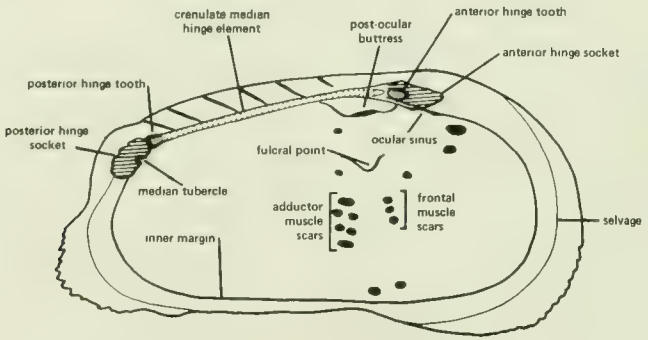


Fig. 1 Internal structure of *Urocythereis*.

Carapace elongate-ovate or sub-rectangular; reticulate or coarsely pitted. Muri foveolate. Valves heavily calcified. Inner lamellar moderately wide. Numerous straight, unbranched radial pore canals. Hinge heterodont often with median tubercle in posterior socket of right valve and with a corresponding lobed tooth in the left valve. In front of the anterior hinge element is a conspicuous, deep ocular sinus and behind is a large solid buttress which bears a large muscle scar.

Two or three frontal muscle scars (not *always* three as stated by Van Morkhoven, 1963, and Hartmann & Puri, 1974); four adductor scars, the centre two of which may be sub-divided. Between these two sets of scars is a deep sub-central depression which corresponds to a flattened sub-central tubercle, externally. Immediately above this depression is a variously developed fulcral point flanked by two small scars and below the sub-central area are two small scars. There are two scars anterior to the ocular sinus, and another just below the buttress (see Fig. 1). Externally, each valve bears a smooth eye tubercle behind which is a conspicuous post-ocular sinus. Dorsal to the hinge, each valve bears a row of oblique elliptical fossae. The two rows of fossae are slightly

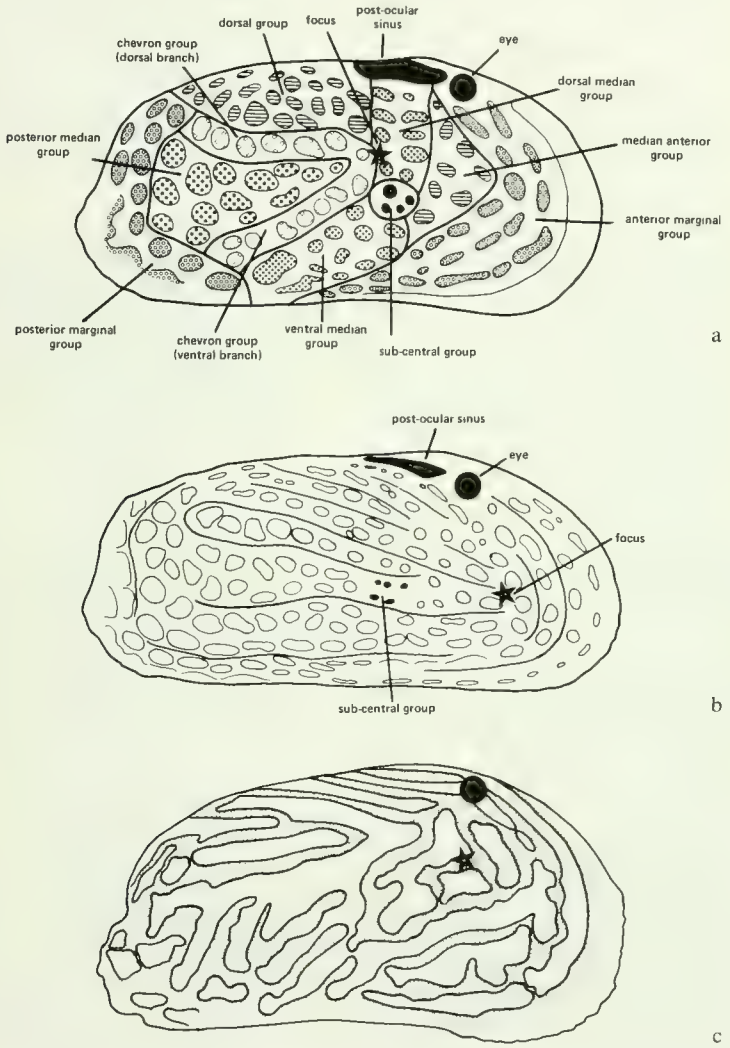


Fig. 2 Fossal pattern and homologous carapace reference points in *Urocythereis* spp. (a) *U. britannica* sp. nov., *U. neapolitana* sp. nov., *U. distinguenda* (Neviani), *U. favosa* (Roemer) and *U. margaritifera* (Müller); (b) *U. seminulum* (Seguenza); (c) *U. lumbricularis* (Terquem). (See pp. 250–252 for explanation.)

offset relative to one another (see Pl. 8, figs 3 & 4). The anterior and posterior margins of the shell are coarsely denticulate. The inner margin and the line of concrescence are coincident and the marginal zone is broad, bearing a prominent selvage half way between the inner and outer margins.

Pores. The numerous normal pores open internally, each in a depression in the shell. Both muri and soli bear the external openings of normal pore canals. In all the Recent species examined, there appear to be two types of pore present. Simple, single pores, supporting single setae which penetrate the surface of the carapace, and 'sieve' pores which are closed by sieve-like perforated plates, bearing sub-central bosses supporting single setae. The simple pores always appear in the muri, the sieve-pores usually in the soli. However, in *U. favosa* (Roemer) sieves have been found in the muri as well as in the soli, and in this species also, the simple mural pores often show the presence of a small sieve deep within the pore canal. However, this was not observed in any other species.

Reticulation. All known species of *Urocythereis* are reticulate. The size of the fossae and the muri vary considerably within the genus and even between members of the same species. The simplest form of reticulation is perhaps that type found in *U. lumbricularis* (Terquem), i.e. simple straight muri with intervening labyrinthic fossae. In other, more highly reticulate species, groups of fossae replace the labyrinths. In such forms, the thickness of the muri increases as the size of the fossae decreases.

Celation. In some species reticulation is accompanied by celation, i.e. the development of a tegmen. The tegmen is formed by secondary growth of the tops of the muri which extend laterally towards each other. They may, in some cases, anastomose and often the underlying fossae are almost entirely obscured. Athersuch & Ruggieri (1975) described the presence of a suprategmen in their *Urocythereis phantastica.* This is a calcareous layer which apparently overlies and often connects adjacent branches of the tegmen. In *Urocythereis*, celation is found only in a few species, all the individuals of which show some signs of tegminal development (e.g. *U. distinguenda* (Neviani), *U. phantastica* Athersuch & Ruggieri), although within one species this is often variable (e.g. *U. distinguenda*).

The mechanism by which the tegmen is formed, and its function, are not known. Benson (1972) suggested that celation allows the development of a strong, yet relatively lightweight, carapace. In *U. distinguenda* at least, tegminal development is not related to depth or any other known ecological factor. Populations from various depths (0–40 m) and locations showed the same range of variation in celation. The development of a tegmen may be a sign of maturity, and perhaps it is only the older adults which possess extremely celate carapaces. The juveniles of this species (at least the last few instars) do show signs of tegminal development, but to a much lesser degree.

Fossal patterns Liebau (1969, 1971), employing an arbitrary notation of fossae was able to illustrate the presence of conservative patterns of the reticulum and pore conuli distributions in *Oertliella* and in the Trachyleberidinae. This system of graphic reduction, which identifies combinations of adjacent fossae, was further developed to study evolutionary trends in *Agrenocythere* and other genera by Benson (1972), who considered the muri, rather than the fossae, as the most significant elements of the reticulum.

Urocythereis can be divided into three groups on the basis of the distribution of fossae. They are:

(1) *U. britannica, U. distinguenda, U. margaritifera, U. favosa, U. neapolitana;*

(2) *U. lumbricularis, U. phantastica;*

(3) *U. seminulum.*

The fossae of *U. britannica, U. distinguenda* and *U. margaritifera* can be divided into nine arbitrary groups, each group having a constant relationship with adjacent ones and with three homologous carapace reference points (eye, post-ocular sinus and sub-central area; see Fig. 2a). The groups are arranged so that variants show no cross-links between groups, only within groups. Within single populations each of these species show variation in the number and size of fossae, one or more small fossae of one specimen often occupying sites homologous with a large fossa of another specimen. Figs 3a f are reticular silhouettes based on specimens *U. britannica, U. distinguenda* and *U. margaritifera* exhibiting the two extremes in ornamental development. The homologous groups are indicated by different symbols shown in Fig. 2a.

(1) Sub-central group: about four small fossae situated on the flattened sub-central tubercle.

(2) Anterior marginal group: consists of two or three rows of fossae frequently linked longitudinally and laterally. The group arises at the eye and terminates beneath the sub-central area.

(3) Dorsal median group: two vertical rows of fossae directly beneath the post-ocular sinus and directed towards the sub-central area.

(4) Median anterior group: a triangular group lying between groups 2 & 3 and terminating at the sub-central area.

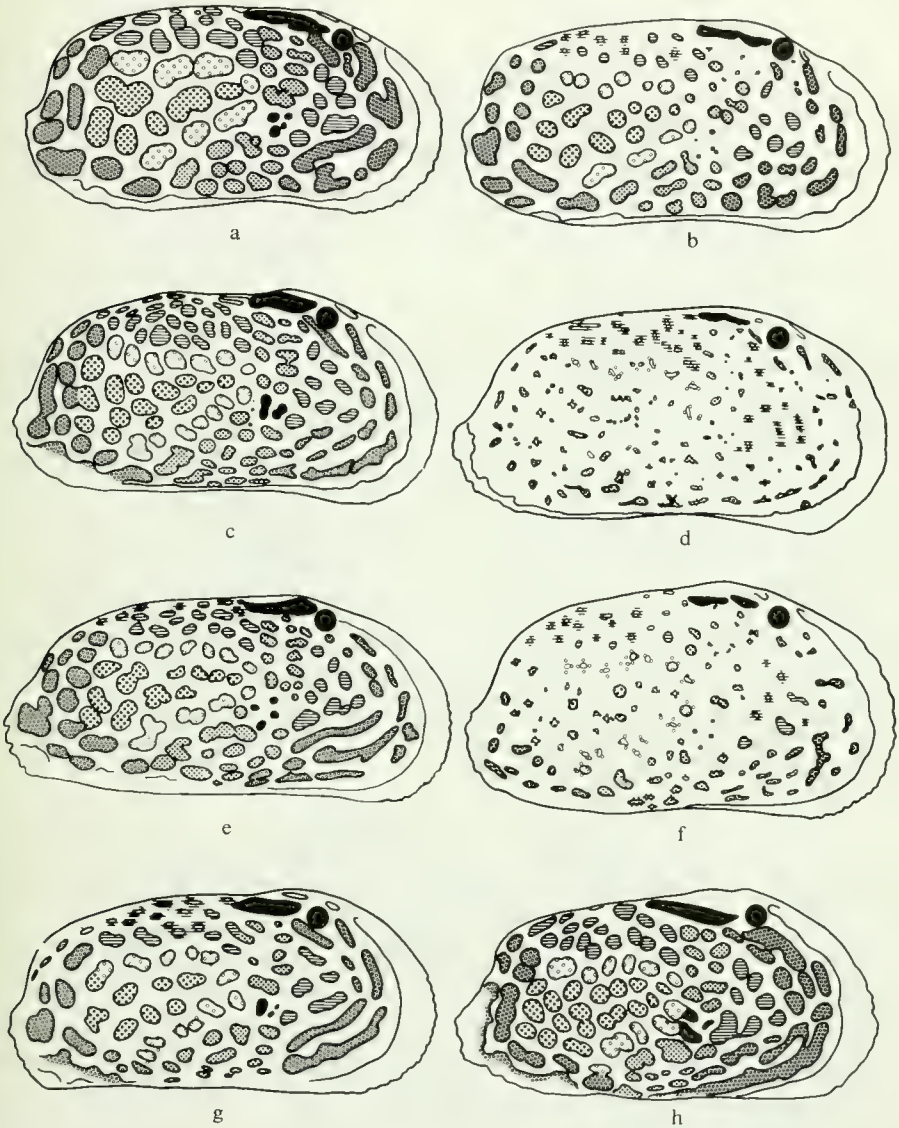


Fig. 3 Fossal patterns in *Urocythereis* spp. (a, b) *U. britannica* sp. nov.; (c, d) *U. distinguenda* (Neviani); (e, f) *U. margaritifera* (Müller); (g) *U. favosa* (Roemer); (h) *U. neapolitana* sp. nov. See Fig. 2a for shading scheme used to delineate fossal groups. For full discussion see pp. 250–252.

(5) Chevron group: The most ventral fossa of group 3 (above) is a point of focus for the two branches of a chevron-shaped group. The end members of this group are adjacent to the end members of group 6.

(6) Posterior marginal group: One or two rows of fossae concentrically arranged around the posterior and postero-ventral margins.

(7) Posterior median group: enclosed by groups 5 & 6.

(8) Dorsal group: this consists of several irregular rows of fossae running sub-parallel to the dorsal branch of group 5.

(9) Ventral median group: enclosed by the anterior marginal group, the sub-central area, the ventral branch of group 5 and end fossa of the posterior marginal group.

Urocythereis favosa and *U. neapolitana* (Figs 3g, h) may also be included in this group, although some slight differences in the fossal pattern can be seen.

There are certain similarities in the arrangement of the fossae of the previous group and the labyrinths of *U. lumbricularis* and *U. phantastica*. For example, in *U. lumbricularis* there are two concentric labyrinths anteriorly, and the dorsal and posterior median groups have a focus above the sub-central area (see Fig. 2c). In general, therefore, the labyrinths may be considered to occupy sites homologous with groups of fossae in other reticulate species.

The few specimens of *U. seminulum* examined indicate that this species has a fundamentally different arrangement of fossae (see Fig. 2b). Whereas in *U. distinguenda*, for example, the posterior fossae show a tendency to converge on a point of focus above the sub-central area, the fossae of *U. seminulum* are arranged in groups, bounded by weak costae, which often pass across the sub-central area and have a focus anterior to the sub-central area. It is possible to recognize dorsal, anterior marginal, posterior median groups and the dorsal branch of the chevron-shaped group. The fossae in the ventral and mid-anterior areas are more linearly arranged than in other species and in the ventral region the fossae are arranged in groups sub-parallel to the ventral margin.

Only a few specimens of *U. flexicauda* and the type illustration of *U. schulzi* were available for comparison, but they also appear to have fossal patterns similar to *U. britannica*. The fossae of *U. colum* are so small and far apart that no definite conclusion regarding the fossal patterns could be drawn. However, this species appears to possess a concentrically arranged anterior group, and ventral and dorsal groups which converge on a focus above the sub-central area.

If the degree of similarity of fossal patterns can be used as an index of genetic relationship, it might be considered possible to divide a genus on the basis of differing fossal patterns. However, at the specific level such a division would have taxonomic significance only if correlated with other morphological differences (e.g. muscle-scars or possession of a tegmen). No such division is possible in *Urocythereis*, for in contrast to the wide variation in ornamentation, the internal structure of the carapace, and morphology of the soft-parts, where known, are remarkably similar in all species.

Appendages of *Urocythereis*

In the following descriptions the terminology used in describing the appendages follows Skogsberg (1928) and Harding & Sylvester-Bradley (1953). The positions and arrangement of the parts of the appendages described always refer to dissected specimens examined under coverslips. The small pili are at the limits of the definition of the transmitted light microscope and some have inevitably been omitted.

First antenna. Strong, 5-jointed. Fourth podomere fused. First podomere hirsute postero-proximally. Second podomere hirsute antero-proximally and mid-posteriorly, with one annular, pilose seta postero-distally. Third podomere bears a stout antero-distal seta. Fourth podomere hirsute antero-proximally, and bearing mid-anteriorly, one stout, anteriorly pilose, and two fine setae, one long, one short. One fine seta is found antero-distally, and a long fine seta and a stout, anteriorly pilose seta are situated terminally (In some specimens of *U. distinguenda*, an additional very small, annulate seta was observed in this position.). Fifth podomere with two short fine, one long fine and one stout, anteriorly pilose seta.

SECOND ANTENNA. Strong, 4-jointed (one protopodite and three endopodite podomeres). Second endopodite podomere fused. 2-jointed expodite well developed, longer and stilleto-like in male, the first joint being shorter and broader in female. Receives duct from large antennal gland. First endopodite podomere hirsute mid-anteriorly and with one long annular, pilose seta postero-distally. Second endopodite podomere long and coarsely bristled posteriorly, with three setae mid-posteriorly, one of which is variously developed. Two fine setae, one long, the other short, occur antero-distally and one fine seta is found postero-distally. Distal podomere with three short, chelate setae.

MANDIBLE. Heavily sclerotized first protopodite podomere forms a strong masticatory process. The base of the large mandibular palp consists of a second protopodite podomere bearing an exopodite with ? four setae distally and two setae ventrally. The proximal one is long, annular and pinnate, the distal one, stout and hirsute. The first endopodite podomere bears four setae ventro-distally, of which two are small and two are long, curved and coarsely pinnate. A similar but larger and more finely pinnate seta is present ventro-distally on the next podomere. The second endopodite podomere bears up to five long, whip-like, naked setae and an annular, pilose seta. The terminal podomere bears three setae, the shortest of which is annular and pilose.

MAXILLA. Posteriorly, the exopodial vibratory plate has 14 long, tapering, pinnate setae with swollen, naked bases. Maxillary palp: three distinct endites of similar dimensions, each bearing up to eight short, curved, naked setae, the exact number of which being difficult to determine. Endopodite 2-jointed, the proximal podomere being larger with four distal setae, of varying length and detailed structure, dorsal to the second podomere which is small and bears three stout, naked, terminal setae swollen basally. Ventral to the second podomere and arising from the distal part of the first podomere is another, similar seta.

LEGS. Long and slender, the second and third pairs being successively larger than the first. The first podomere of each bears a short, annular seta which may also be pilose or hirsute postero-proximally. Mid-anteriorly the first and second legs bear two long, annular, usually pilose, setae. The third leg has only one such seta. Antero-distally, the first leg has two annular, pilose setae, whereas the second and third legs have only one. Each leg bears a short, often pilose seta antero-distally on the second podomere and each leg tends to develop short bristles distally along the anterior margins of the second to fourth podomeres.

THE BRUSH-SHAPED ORGANS. Simple, unjointed and sub-quadrangular with about 15 long, whip-like setae terminally.

MALE COPULATORY APPENDAGES. Complex, with large oval, articulating chitin framework with transverse musculature proximally. Triangular distal portion with acute terminal 'lappet' and prominent, thickened *ductus ejaculatorius* which may be retained within the structure of the appendage or extend freely to varying degrees, ventrally. The rest of the structure is difficult to define. This appendage, which defies accurate written description, is probably the most important single appendage used in delimiting individual species.

Intraspecifically, the soft-part characters are more stable than those of the carapace. Where possible, initial specific identification should be made using the soft-parts. The greatest inter-specific variation occurs in the structure of the male copulatory appendages which Skogsberg (1928) considered as the primary seat of evolution and basic to delineation of species. The differences lie mainly in the varying size and shape of the distal 'lappet' and the course of the *ductus ejaculatorius*. For instance, a comparison of the lappets of the copulatory appendages of *U. britannica* (Fig. 4a) and *U. margaritifera* (Fig. 4d) shows that in the former the ventral margin is straight whereas in the latter it is incurved; also, the lappet is generally broader and has a curved dorsal margin. In contrast to these two species, the copulatory appendages of *U. flexicauda* (Fig. 4e), as well as being smaller overall than those of any of the other species examined, possess long lappets with almost parallel sides. The course of the *ductus ejaculatorius* also varies consi-

derably within the genus. For instance, in *U. britannica* and *U. margaritifera* the duct is short and is contained within the area of the appendage; in *U. distinguenda* (Fig. 5i) the duct is much longer and passes beyond the ventral margin. In *U. neapolitana* (Fig. 6e) it is extremely long and extends far beyond the ventral margin in a broad loop. In addition, a group of three setae, found posteriorly on the second endopodite podomere of the second antennae, are differently developed in each species. Other characters of the soft-parts which appear to be diagnostic of individual species include the relative and absolute sizes of the podomeres and setae. The appendages of five species of *Urocythereis* are illustrated in Figs 4–6.

Stratigraphical distribution

Of the seven species of *Urocythereis* known to be living in the Mediterranean only one has, without doubt, a fossil occurrence (i.e. *U. phantastica* Athersuch & Ruggieri). The Recent British species, *U. britannica* Athersuch, has not been recorded living from the Mediterranean but appears to have been in this region during Pliocene and sub-Recent times. Other fossil forms, known only from the Mediterranean region, e.g. *U. favosa*, *U. lumbricularis*, *U. seminulum*, do not appear to have living representatives, although there is some evidence to suggest that *U. favosa* may have Recent (? sub-Recent) representatives (Doruk, 1974).

Remarks

At present in the Mediterranean, this genus appears to be a large and diverse one and it is probable that in the past there were more species than we have as yet clearly distinguished amongst the available material.

Ascribing names of Recent species to fossil forms has been a misleading, but common, practice in many previous studies of this genus and has done much to confuse the taxonomy.

Future research on this genus must include collection of living material from many more Mediterranean and NW European localities (particularly in N. Africa, see Pl. 17) and a systematic study of the fossil forms.

Systematic descriptions

Although the primary purpose of this study has been a revision of the Recent species of *Urocythereis*, it was thought essential to include a description and illustrations of the type-species (*U. favosa*) from the Pliocene of Italy to obtain a fuller understanding of the generic concept of *Urocythereis*. Moreover, to show the range of morphological variation within the genus, two other fossil forms, *U. lumbricularis* (Terquem) and *U. seminulum* (Seguenza), are described and illustrated herein. The synonymy listed for each species is not intended to be complete. Only original citations, changes of name and other references of major importance have been included.

The distributions given for each species are those verified by the present author, usually from original material, but occasionally from descriptions and illustrations alone. Fig. 8, at the end of this work, shows a distribution map of the Recent species of *Urocythereis*.

Sub-class **OSTRACODA** Latreille, 1802 (nom. correct., Latreille 1806)
Order **PODOCOPIDA** Müller, 1894
Sub-order **PODOCOPA** Sars, 1866
Family **HEMICYTHERIDAE** Puri, 1953
Sub-family **UROCYTHEREIDINAE** Hartmann & Puri, 1974
Genus ***UROCYTHEREIS*** Ruggieri, 1950

TYPE-SPECIES. (Original designation) *Cytherina favosa* Roemer, 1838.

The references cited in the following synonymy of *U. favosa* have been restricted to those which refer to material obtained from the type-locality only. A future revision of fossil representatives of this genus may result in the addition of further references. For details of other citations of *U. favosa*, see Ruggieri (1950) and Doruk (1974).

Urocythereis favosa (Roemer)

(Pl. 1, fig. 1; Fig. 3g)

Cytherina favosa sp. nov. Roemer, 1838 : 516, pl. 6, fig. 7.
Urocythereis favosa (Roemer); Ruggieri, 1950 : 28, pl. 1, fig. 4, text-figs 10–14.
Urocythereis favosa (Roemer); Doruk, 1974 : 33, 34, figs 1–3; 36, fig. 2; 38, fig. 1; 42, fig. 1; 44, fig. 1. (?) 36, figs 1, 3; 38, figs 2, 3; 40, figs 1–3; 42, figs 2–5, 44, figs 2–3.

NEOTYPE. (?) Male left valve; B.M.(N.H.) no. I0 5855.

TYPE-LOCALITY. Castellarquato, N. Italy: approx. 44°51′ N, 09°52′ E; Pliocene.

DIAGNOSIS. No formal diagnosis is given here as it is felt that too few specimens have been examined.

REMARKS. Roemer first described *Cytherina favosa* in 1838 from the Pliocene of Castellarquato, Italy. This species was chosen by Ruggieri in 1950 as the type-species for his new genus *Urocythereis*. He illustrated topotypic material, since Roemer's original specimens are presumed lost. This description was amplified by Doruk (1974) who demonstrated the apparently wide range of fossal development of this species. However, Pliocene forms illustrated have big fossae, and central tubercles occur in the posterior hinge element of the left valve, whereas (sub-)Recent forms have small fossae and lack central tubercles. There are also differences in shape between the two forms. Although *U. distinguenda* clearly demonstrates that even within one population, extreme variation of ornament may occur, it is probable that the forms described by Doruk represent two species, one Pliocene, the other (sub-)Recent.

Many reticulate fossil species, with large rounded fossae, have been recorded as *U. favosa* (Roemer). It is likely that many of these descriptions refer to other, as yet undescribed, species. Other species such as *Cythere sorocula* Seguenza and *Cythere mirabilis* Brady *sensu* Capeder may be synonymous with *U. favosa*. A further study of fossil specimens from the Mediterranean area is now essential.

This species is distinct from any known Recent species from the Mediterranean, and all known references to Recent *U. favosa* are probably incorrect as it is presumed extinct.

FIGURED SPECIMEN. A ? male specimen from Roemer's type-locality, collected by Professor G. Ruggieri, is here proposed as a neotype for this species.

Urocythereis britannica sp. nov.

(Pl. 1, figs 4–6; Pl. 2, figs 1–6; Pl. 3, figs 1–6; Pl. 4, figs 1–5; Figs 3a, b; 4a–c, g)

Cythere oblonga Brady, 1868; 400, pl. 31, figs 14–17. (non *C. oblonga* Brady, 1866 (= *Urocythereis distinguenda* (Neviani))).
Urocythereis oblonga (Brady); Wagner, 1957 : 63, pl. 26, figs 1–5.
Paracythereis oblonga (Brady); de Vos, 1957 : 34, pl. 15, figs 1a–h.
? *Urocythereis margaritifera margaritifera* (Müller); Sissingh, 1972 : 128, pl. 10, fig. 8.

HOLOTYPE. Male carapace and soft parts B.M.(N.H.) no. 1976.1041.

PARATYPES. Both sexes B.M.(N.H.) nos 1976.1043–50, 1052.

TYPE-LOCALITY: Poole, Dorset, England; Recent.

DIAGNOSIS: Oblong, rounded and sub-rounded fossae in consistent pattern. Obliquely rounded posterior margin. Muri excavate and foveolate. Male copulatory appendages diagnostic.

DERIVATION OF NAME. Latin, '*Britannica*' – British (refers to its frequent occurrence on British coasts).

DISTRIBUTION: Recent; (as *U. oblonga* (Brady)) – Bay of Biscay, S. Wales (Brady collection, Hancock Museum), S. England, N. Spain and France (author's collection), Heligoland (Remane collection). Holocene; Netherlands (Wagner, 1957). (?) Pliocene; Aegean (Sissingh, 1972). (?) sub-Recent; Cyprus (author's collection).

Fig. 4 Appendages of *Urocythereis* spp. (a) *U. britannica* sp. nov., ♂ left copulatory appendage (×208); (b) *U. britannica* sp. nov., ♂ left second antenna (×208); (c) *U. britannica* sp. nov., ♂ left first antenna (×208); (d) *U. margaritifera* Müller, ♂ left copulatory appendage (×250); (e) *U. flexicauda* Bonaduce, Ciampo & Masoli, ♂ left copulatory appendage (×300); (f) *U. margaritifera* Müller, ♂ right first antenna (×250); (g) *U. britannica* sp. nov., ♂ mandible (×208); (h) *U. margaritifera* Müller, ♂ left second antenna (×250).

Remarks. The fossae are extremely variable in size, and in some specimens no fossae are developed over parts of the carapace (see Pl. 2, fig. 4). Massive anterior reticular field. The specimens from Heligoland show ghost reticulation and have a subdued ornament. Posterior element of the hinge of the left valve may possess a median tubercle, and the posterior element of the right valve may be correspondingly lobed. Sexual dimorphism slight: males larger than females more quadrangular and more inflated posteriorly. Fulcral point often pessular.

Both this species and *U. distinguenda* have often been recorded erroneously under the name *U. oblonga* (Brady) (junior objective homonym of *C. oblonga* M'Coy, 1844). Their shapes are, however, quite distinct and in addition *U. distinguenda* develops a tegmen which is lacking in *U. britannica*. The soft parts, particularly the male copulatory appendages, are distinct. *Hemicythere oblonga* (Brady) *sensu* Sars from Scandinavia is probably conspecific with the present species (see Pl. 1, figs 4–6).

Figured specimens. B.M.(N.H.) nos 1976.1041, 1043–1050, 1052 were collected alive by C. P. Palmer from beach sand, Shell Bay, $\frac{3}{4}$ mile S of Poole Harbour, Dorset, England, approx. 50°42′ N, 02°00′ W, during August 1975.

No. 1976.1042, from the Brady collection in the B.M.(N.H.) is from the Gulf of Gascogny, SW France.

No. 1976.1051 was collected by Squ. Lrd C. R. Chrisp from Akrotiri Bay, Cyprus, approx. 34°34′ N, 33°02′ E, during 1968. Nos K30467 a–c were collected by A. Remane from Heligoland during 1933 and are housed in the Zoological Museum, Hamburg.

Urocythereis colum sp. nov.

(Pl. 5, figs 1–6; Pl. 6, figs 1–5)

Holotype. Male left valve B.M.(N.H.) no. 1976.1066.

Paratypes. Valves and carapaces of both sexes B.M.(N.H.) Nos 1976.1067–70.

Derivation of name. Latin, colum (used in apposition) – a colander; refers to appearance of carapace, perforated by large, circular normal pores.

Type-locality. Dhavlos Bay, Cyprus.

Diagnosis. Numerous small, circular, widely separated fossae arranged in a consistent pattern. The soli of most fossae are occupied by large sieve plates. Surface foveolate.

Distribution. Known only from Cyprus (author's collection), where it occurs infrequently in shallow water sands.

Remarks. The sizes of the homologous fossae are consistent in the specimens examined. Males with well-preserved soft-parts unknown.

Figured specimens. All the specimens are from beach sands in Cyprus. Nos 1976.1067, 1068 were collected by J. Athersuch during April 1973 from Khelones Bay, approx. 35°36′ N, 34°26′ E. Nos 1976.1066, 1069 and 1070 were collected by Professor P. C. Sylvester-Bradley during summer 1972 from Dhavlos Bay, approx. 33°35′ N, 35°27′ E.

Urocythereis distinguenda (Neviani)

(Pl. 7, figs 1–6; Pl. 8, figs 1–6; Pl. 9, figs 1–5; Pl. 12, figs 5, 6; Figs 3c d; 5a–i)

Cythere oblonga sp. nov. Brady, 1866 : 353, pl. 59, figs 5a–d (*non C. oblonga* M'Coy, 1844).
Cythereis (*Auris*) *distinguenda* nom. nov. Neviani, 1928 : 105 (synonymy only); (*non* p. 105 description and pl. 2, figs 91–93).
Urocythereis aff. *U. favosa* (Roemer); Bonaduce, Ciampo & Masoli, 1975 : p. 45, pl. 22, fig. 8 (*sic* fig. 7).

Neotype. A female carapace and soft-parts B.M.(N.H.) no. 1976.1031.

Paratypes. Both sexes B.M.(N.H.) nos 1976.1026–30, 1032–40, 1074.

Type-locality. Kyrenia, Cyprus, approx. 35°19′ N, 33°19′E; Recent.

Fig. 5 Appendages of *Urocythereis distinguenda* (Neviani) (×208). (a) ♂ right first antenna; (b) ♂ right second antenna; (c) ♂ mandible; (d) ♂ maxilla; (e) ♂ brush-shaped organ; (f) ♂ left third leg; (g) ♂ right second leg; (h) ♂ right first leg; (i) ♂ right copulatory appendage.

DIAGNOSIS. A species of *Urocythereis* with deep fossae showing varying degrees of celation. Extreme development of the foveolate tegmen may obscure the underlying fossae, and leave many small, widely spaced pits. Male copulatory appendages diagnostic.

DISTRIBUTION. The taxonomy of this species has been always confused and it is impossible to judge from past literature which of the many records of *U. oblonga*, *U. favosa*, *U. distinguenda* and *U. margaritifera*, if any, refer to this species. The following records can be confirmed. Recent; Cyprus (author's coll.), Greece (B.M.(N.H.) coll.), the Levant (Brady, 1866), Nota Marina, Sicily, and Puglia, Italy (author's collection). Living specimens found in coarse sand at 0–40 m.

REMARKS. Neviani (1928) provided a new name for Brady's species, *Cythere oblonga*, a junior objective homonym of *C. oblonga* M'Coy, 1844, and also illustrated and re-described the species using his own material from the Pliocene of Italy. I consider that the specimens of Brady and of Neviani are not conspecific. However, *Cythereis distinguenda* remains the next available name for Brady's species. Unfortunately, no specimens attributable to this species remain in the Brady collection at the Hancock Museum, Newcastle-upon-Tyne, or at the British Museum (Natural History) and therefore a neotype has been selected from Cyprus, geographically close to Brady's Levant localities.

Brady himself considered that this species was conspecific with the form now recognized as *U. britannica* sp. nov. (herein) as he illustrated both species as *C. oblonga* (see Brady, 1868 : pl. 31).

Males more quadrangular, more elongate and more inflated posteriorly than females.

FIGURED SPECIMENS: B.M.(N.H.) nos 1976.1026, 1028, 1034, 1038 collected by J. Athersuch during April 1973 from Khelones Bay, Cyprus (approx. 35°36′ N, 34°26′ E), in beach sand.

Nos 1976.1027, 1029–31, 1037, 1074 collected by J. Athersuch from Cyprus during Autumn 1973. All specimens were living or contained remnants of soft-parts when collected. Nos 1976.1027, 1029, 1074 from Cape Greco (approx. 34°58′ N, 34°05′ E) in sand at 12 m, water temp. 22 °C. No. 1976.1030 from Famagusta Bay (approx. 35°08′ N, 33°56′ E) in sand at 13 m, water temp. 26 °C, pH 8·2, O_2 107%. No. 1976.1031 from Kyrenia (approx. 35°19′ N, 33°19′ E) in sand at 5 m, water temp. 26 °C. No. 1976.1037 from Famagusta (approx. 35°08′ N, 33°58′ E) in sand.

Nos 1976.1032, 1033, 1035, 1036, 1040 collected by Squ. Ldr C. R. Chrisp from sand 0–7 m in Akrotiri Bay, Cyprus (approx. 34°34′ N, 33°02′ E), during 1968.

Nos 1976.1039 collected by Dr W. Chaster from Delos, Greece, approx. 37°23′ N, 25°17′ E (ex- B.M.(N.H.) no. 1963·4·26·6).

Urocythereis flexicauda Bonaduce, Ciampo & Masoli

(Pl. 10, figs 1–6; Pl. 11, figs 1–5; Fig. 4e)

Urocythereis flexicauda sp. nov. Bonaduce, Ciampo & Masoli, 1975 : 45, pl. 22, figs 1–6.

HOLOTYPE. Single left valve; Bonaduce, Ciampo, Masoli collection no. 225; Zoological Museum, Naples.

PARATYPES. Two valves, B.C.M. collection no. 226.

TYPE-LOCALITY. Apulia coast of the Adriatic Sea, Italy.

DIAGNOSIS. A species of *Urocythereis* with enlarged and depressed postero-ventral region, bearing large labyrinthic fossae. Postero-ventral margin obliquely rounded. Male copulatory appendages diagnostic.

REMARKS. Only one live specimen (male) has been found (Apulia, Adriatic coast of Italy). This species is extremely rare and has been recorded only from the coasts of Italy. The shape of the valves varies considerably and the fossae, which are in a consistent pattern, are variously developed.

DISTRIBUTION. Recent; Adriatic (Bonaduce, Ciampo and Masoli, 1975 and author's collection); Crotone and Naples, Italy (author's collection).

FIGURED SPECIMENS. All the specimens were collected from the coasts of Italy. Nos 1976.1055, 56,

58 were collected by Professor G. Ruggieri from beach sands at Crotone, approx. 39°05′ N, 17°15′ E.

No. 1976.1054 from Apulia, SE Italy, and 1976.1057 from Naples, approx. 40°50′ N, 14°18′ E, were kindly given by Dr G. Bonaduce.

Urocythereis lumbricularis (Terquem)

(Pl. 1, fig. 3; Fig. 2c)

Cythere lumbricularis sp. nov. Terquem, 1878 : 105, pl. 12, figs 6a–c.
Urocythereis labyrinthica sp. nov. Uliczny, 1969 : 63, pl. 4, fig. 6; pl. 15, figs 5–7.
Urocythereis lumbricularis (Terquem); Sissingh, 1972 : 128, pl. 10, fig. 7.
Urocythereis labyrinthica Uliczny; Doruk, 1974 : 49–52.

LECTOTYPE. (?) Male, right valve picked from topotypic material collected by Terquem; no registration number, but placed in a separate, labelled slide with the Terquem collection and housed in the Laboratory of Micropalaeontology, Museum of Natural History, Paris.

TYPE-LOCALITY. Rhodes; (?) Pliocene (see Sissingh, 1972).

DISTRIBUTION. Pliocene; Kephalinia, Greece (Uliczny, 1969), Rhodes (Terquem, 1878); Pleistocene (Calabrian); Italy (Doruk, 1974).

REMARKS. Terquem (1878) commented that there was considerable variation in the ornament of *Cythere lumbricularis*. However, the specimens obtained from the Terquem collection have a consistent pattern, similar to that of the lectotype. Uliczny (1969) recognized two sub-species of *Urocythereis labyrinthica* on the basis of shape differences of the labyrinths, but Doruk (1974) argued that the variation in the labyrinthic patterns of this species was continuous and that there was no evidence of sub-specific differentiation.

Urocythereis margaritifera (Müller)

(Pl. 12, figs 1–4; Pl. 13, figs 1–6; Pl. 14, figs 1–5; Figs 3e, f; 4d, f, h)

Cythereis margaritifera sp. nov. Müller, 1894 : 368, pl. 32, figs 26, 29, 32, 35–37.

LECTOTYPE. A male carapace and soft-parts from G.W. Müller's syntype collection (no. 9296); no catalogue numbers but placed in separate, labelled slides and housed with the Müller collection (Berlin).

PARATYPES. A large number of males, females and juveniles remain well preserved in the Müller collection (no. 9296).

TYPE-LOCALITY. Bay of Naples, Italy; Recent.

DIAGNOSIS. Irregular, small, rounded, widely separated fossae in a consistent pattern. Male copulatory appendages diagnostic.

DISTRIBUTION. This species in only known from the type-locality, where it was found associated frequently with sand at about 10 m.

REMARKS. Müller (1894) recorded this as one of the most numerous species in the Bay of Naples. However, no specimens referable to this species have been found during recent sampling programmes (pers. comm. G. Bonaduce).

Males more elongate and less inflated than females. Six adductor and three frontal scars; fulcral point pointed. There is a tendency for the posterior element of the right hinge to develop a slight median tubercle and for the posterior element of the left hinge to be correspondingly lobed.

U. margaritifera sensu Uliczny (1969) and *sensu* Sissingh (1972) probably represent one or more fossil species closely related to *U. margaritifera* s.s., but displaying different development of the fossae.

Fig. 6 Appendages of *Urocythereis neapolitana* sp. nov. (×208). (a) ♀ right first antenna; (b) ♀ left second antenna; (c) ♀ mandible; (d) ♀ maxilla; (e) ♂ right copulatory appendage; (f) ♀ left third leg; (g) ♀ left second leg; (h) ♀ left first leg.

FIGURED SPECIMENS. All the specimens were taken from the G. W. Müller collection (ex.-no. 9296); no catalogue numbers, but placed in separate slides labelled (ex-9296 a–g), and housed in the Crustacea Division, Zoological Museum, E Berlin.

Urocythereis neapolitana sp. nov.

(Pl. 15, figs 1–6; Pl. 16, figs 1–5; Pl. 17, figs 1, 3; Figs 3h; 6a–h)

HOLOTYPE. Male carapace and soft parts B.M.(N.H.) no. 1976.1063.

PARATYPES. Carapaces and soft parts of both sexes B.M.(N.H.) nos 1976.1059–65.

TYPE-LOCALITY. Ischia, Bay of Naples, Italy, approx. 40°45′ N, 13°50′E.

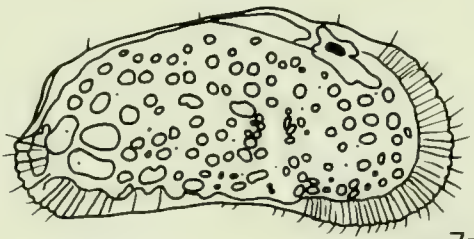
DIAGNOSIS. Large, deep, sub-rounded fossae in a consistent pattern. Smooth, excavate muri. Male copulatory appendages diagnostic.

DERIVATION OF NAME. Latin, '*Neapolis*' – Naples, the type-locality.

DISTRIBUTION. Known only from the type-locality.

REMARKS. In some specimens the fossae are large and the muri are reduced and form a reticulum. Two frontal muscle scars. Fulcral point pointed.

FIGURED SPECIMENS. All the specimens were collected by Dr G. Bonaduce from the Bay of Naples, Italy, depth approx. 50 m, in sand.



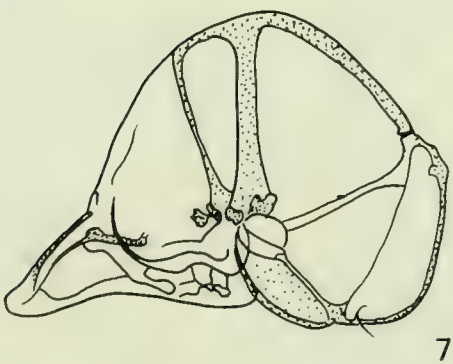


Fig. 7 *Urocythereis schulzi* (Hartmann). (a) ♂ right valve; (b) copulatory appendage. (Both figures after Hartmann, 1958, who gives no indication of size or magnification.)

Urocythereis phantastica Athersuch & Ruggieri

(Pl. 17, fig. 6)

Urocythereis phantastica sp. nov. Athersuch & Ruggieri, 1975 : 223–230.

HOLOTYPE. Female carapace B.M.(N.H.) no. 1974.755a, b.

TYPE-LOCALITY: SE coast of Cyprus, approx. 35°26′ N, 34°04′ E; Recent.

DIAGNOSIS. Muri high, often discontinuous, normally bearing a well-developed tegmen which forms short, angular, occasionally anastomosing branches.

DISTRIBUTION. Known only from the Lower Calabrian and Sicilian (Lower Pleistocene) in Sicily, and Recent in Cyprus. Possibly also occurs Recent in Tunisia.

REMARKS. For full description of the features of the tegmen see Athersuch & Ruggieri (1975).

FIGURED SPECIMEN. Holotype from coarse shell sand; depth 13 m, salinity 39‰, water temperature 23 °C.

Urocythereis schulzi (Hartmann)

(Figs 7a, b)

Paracythereis schulzi sp. nov. Hartmann, 1958 : 230, pl. 36, figs 20–30.

REMARKS. This species was originally described from the Mediterranean coast of France and, as far as I am aware, does not appear to have been recorded subsequently. The type-specimens are lost (pers. comm. Hartmann) and no other material is available. A full diagnosis and illustrations of this species appear in Hartmann (1958).

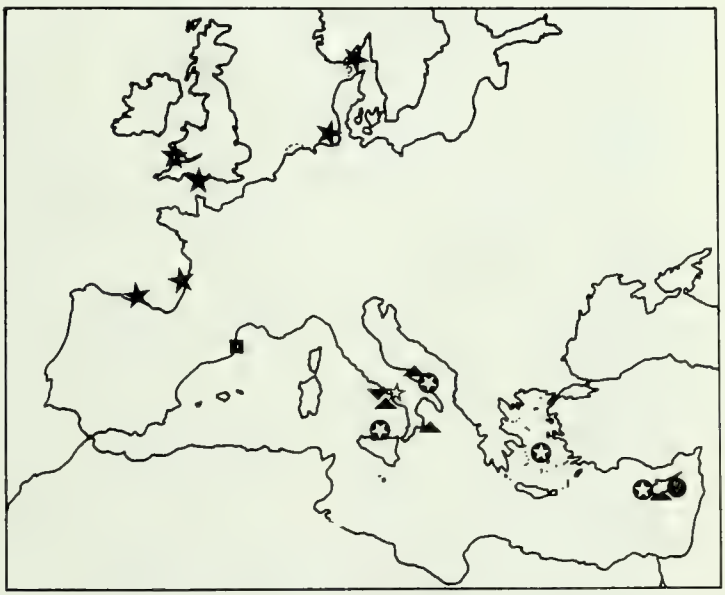


Fig. 8 Distribution of Recent species of *Urocythereis*. ✪ – *U. distinguenda* (Neviani). ★ – *U. britannica* sp. nov. ☆ – *U. margaritifera* (Müller). ▼ – *U. neapolitana* sp. nov. ● – *U. colum* sp. nov. ▬ – *U. phantastica* Athersuch & Ruggieri. ▲ – *U. flexicauda* Bonaduce, Ciampo & Masoli. ■ – *U. schulzi* (Hartmann). (With the exception of *U. schulzi* (see p. 263), only records of living material, verified by the present author, are shown.)

Urocythereis seminulum (Seguenza)

(Pl. 1, fig. 2; Fig. 2b)

Cythere seminulum sp. nov. Seguenza, 1880 : 124, pl. 12, figs 4, 4a.
Urocythereis seminulum (Seguenza); Ruggieri, 1963 : 6, pl. 1, figs 11, 11a, text-fig. 3.
Urocythereis seminulum (Seguenza); Doruk, 1974 : 45–48.

Remarks. For further information about this species see Ruggieri (1963) and Doruk (1974). See also pp. 252, 254.

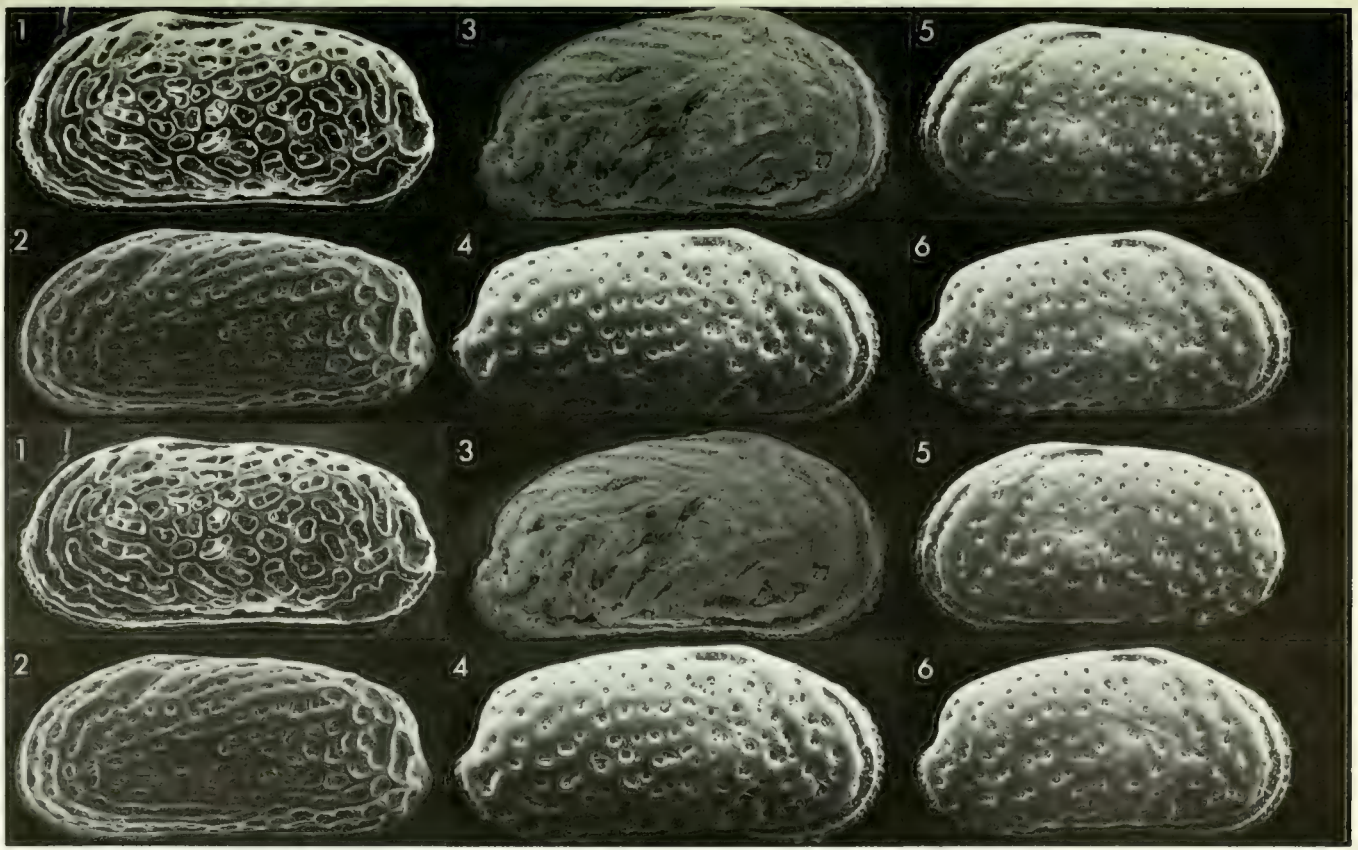


Plate 1 **Fig. 1** *Urocythereis favosa* (Roemer); neotype, B.M.(N.H.) no. I0 5855 (×69); **Fig. 2** *Urocythereis seminulum* (Seguenza); ♂ LV; B.M.(N.H.) no. I0 5848 (×83); **Fig. 3** *Urocythereis lumbricularis* (Terquem); lectotype, Paris Museum of Natural History specimen (×65); *Urocythereis britannica* sp. nov. (×60) **Fig. 4** *Urocythereis britannica* sp. nov. (×60) ♂ RV; Hamburg Zoological Museum no. K30467a; **Fig. 5** *Urocythereis britannica* sp. nov. (×60) ♀ LV; Hamburg Zoological Museum no. K30467b; **Fig. 6** *Urocythereis britannica* sp. nov. (×60) ♀ RV; Hamburg Zoological Museum no. K30467c. (All figures are stereo-pairs.)

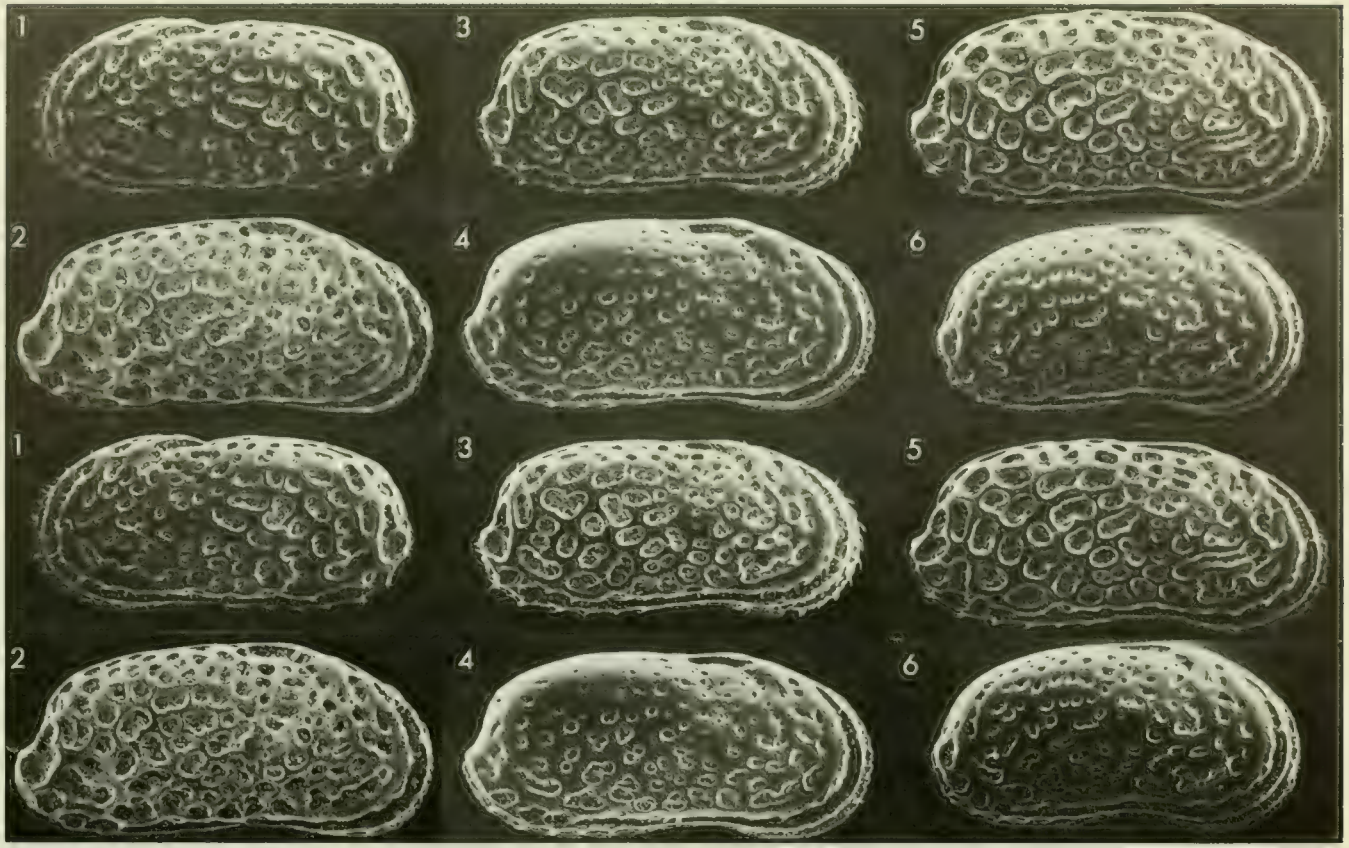


Plate 2 *Urocythereis britannica* sp. nov. (× 64). **Fig. 1** holotype, ♂ LV; B.M.(N.H.) no. 1976.1041; **Fig. 2** ? ♂ RV; B.M.(N.H.) no. 1976.1042; **Fig. 3** holotype, ♂ RV; B.M.(N.H.) no. 1976.1041; **Fig. 4** ♂ RV; B.M.(N.H.) no. 1976.1043; **Fig. 5** ♂ RV; B.M.(N.H.) no. 1976.1044; **Fig. 6** ♀ RV; B.M.(N.H.) no. 1976.1045. (All figures are stereo-pairs.)

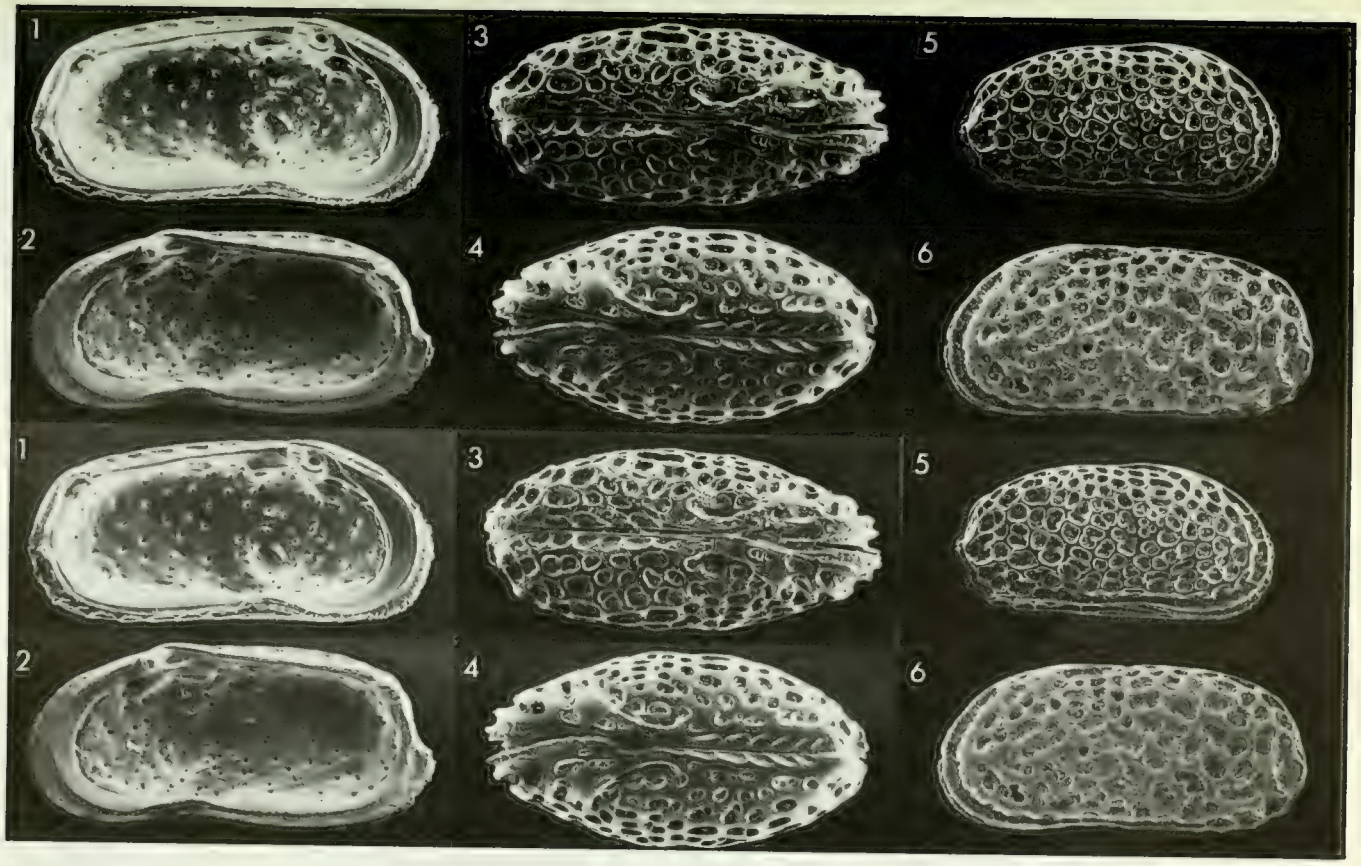


Plate 3 *Urocythereis britannica* sp. nov. (×64). **Fig. 1** ♂ LV; B.M.(N.H.) no. 1976.1046; **Fig. 2** ♂ RV; B.M.(N.H.) no. 1976.1047; **Fig. 3** ♂ dorsal carapace; B.M.(N.H.) no. 1976.1048; **Fig. 4** ♀ dorsal carapace; B.M.(N.H.) no. 1976.1049; **Fig. 5** juvenile (–1) RV; B.M.(N.H.) no. 1976.1050; **Fig. 6** ? sex LV; B.M.(N.H.) no. 1976.1051. (All figures are stereo-pairs.)

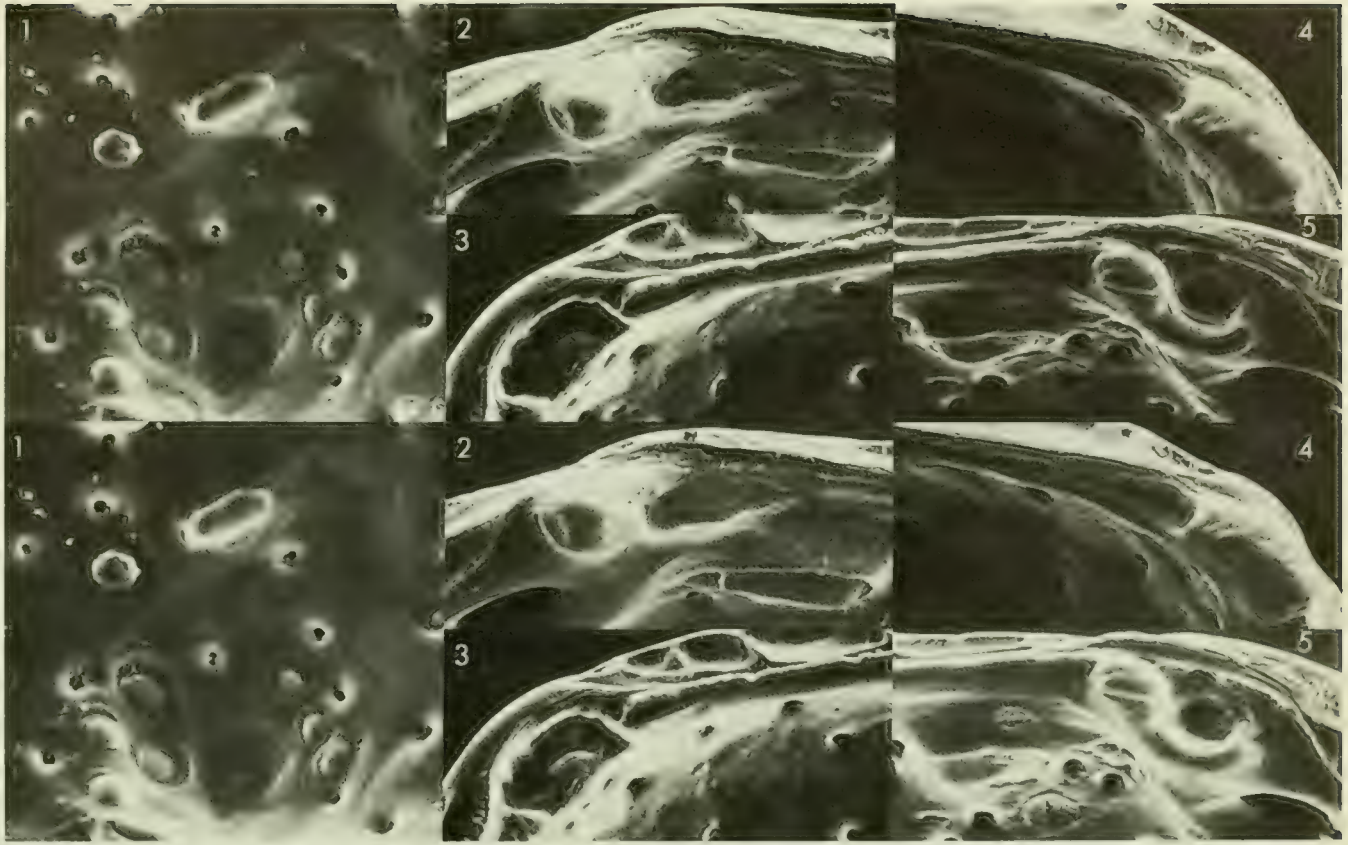


Plate 4 *Urocythereis britannica* sp. nov. **Fig. 1** ♂ LV muscle scars; B.M.(N.H.) no. 1976.1052 (× 255); **Figs 2, 4** ♂ RV, terminal hinge elements; B.M.(N.H.) no. 1976.1047 (× 218); **Figs 3, 5** ♂ LV, terminal hinge elements; B.M.(N.H.) no. 1976.1046 (× 218). (All figures are stereo-pairs.)

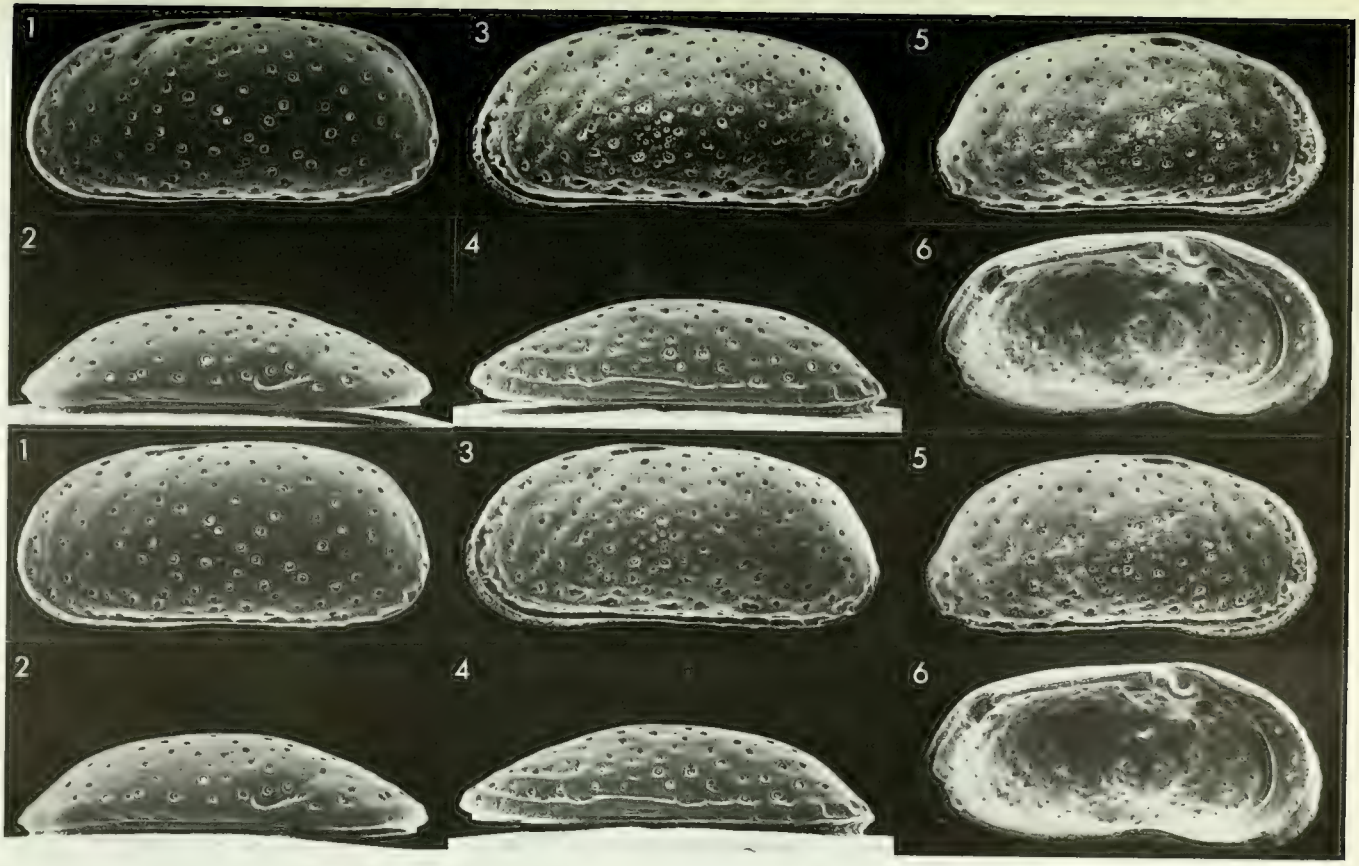


Plate 5 *Urocythereis colum* sp. nov. (×66). **Fig. 1** holotype, ♂ LV; B.M.(N.H.) no. 1976.1066; **Fig. 2** holotype, ♂ dorsal LV; B.M.(N.H.) no. 1976.1066; **Fig. 3** ? sex LV; B.M.(N.H.) no. 1976.1067; **Fig. 4** holotype, ♂ ventral LV; B.M.(N.H.) no. 1976.1066; **Fig. 5** ? sex RV; B.M.(N.H.) no. 1976.1068; **Fig. 6** ? ♂ LV; B.M.(N.H.) no. 1976.1069. (All figures are stereo-pairs.)

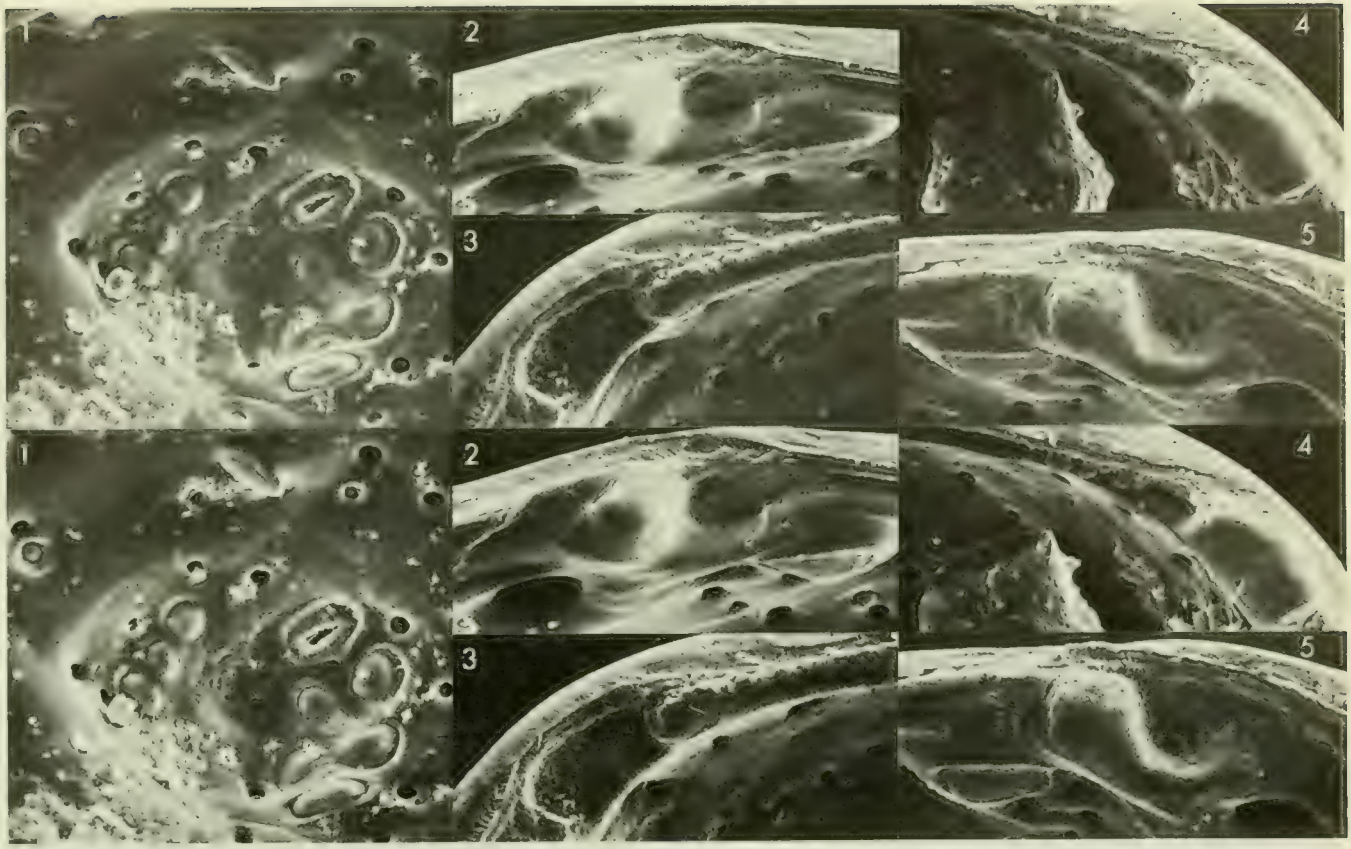


Plate 6 *Urocythereis colum* sp. nov. **Fig. 1** ♀ LV, muscle scars; B.M.(N.H.) no. 1976.1070 (×270); **Figs 2, 4** ♀ RV, terminal hinge elements; B.M.(N.H.) no. 1976.1070 (×255); **Figs. 3 5** ♂? LV, terminal hinge elements; B.M.(N.H.) no. 1976.1069 (×255). (All figures are stereo-pairs.)

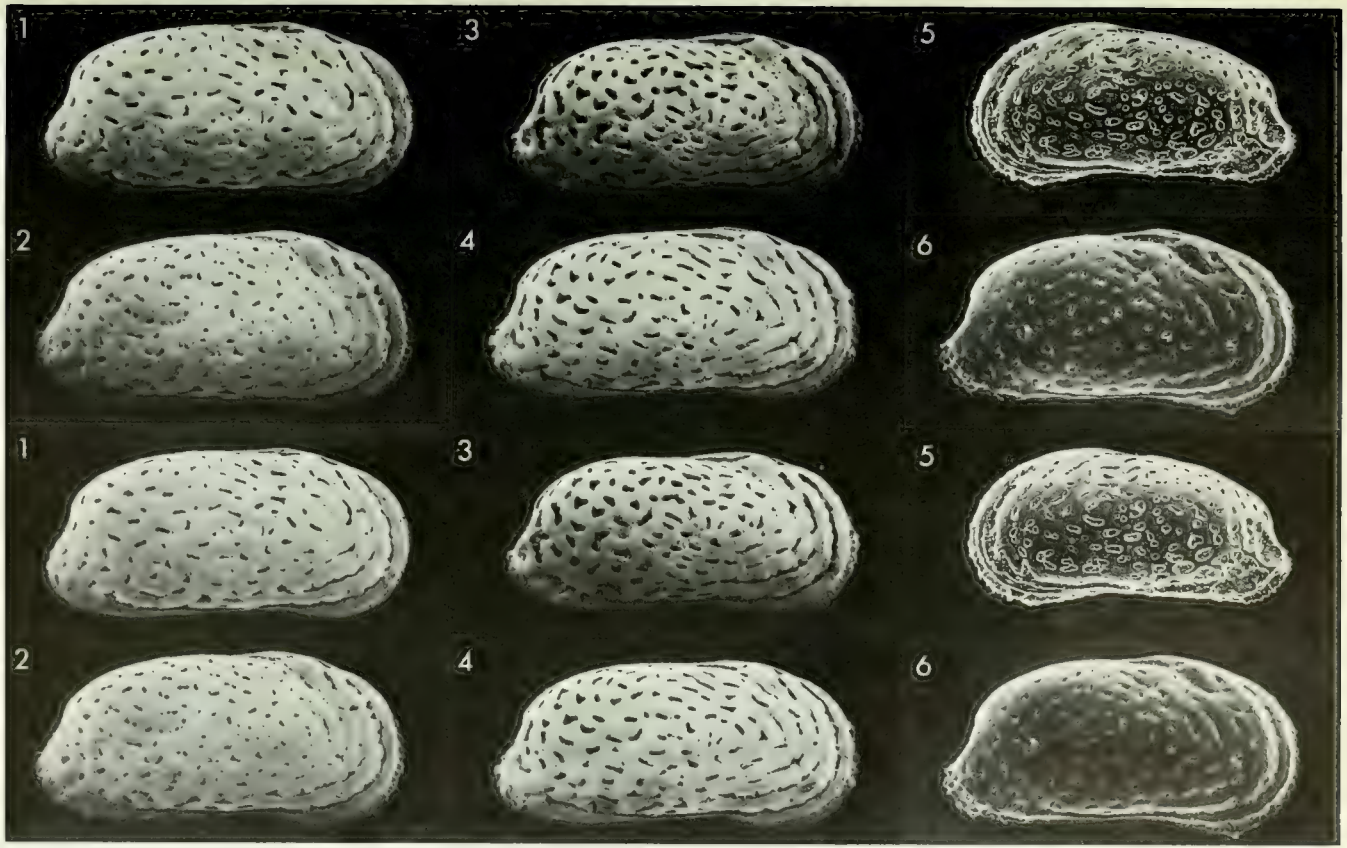


Plate 7 *Urocythereis distinguenda* (Neviani) (×60). **Fig. 1** ♂ RV; B.M.(N.H.) no. 1976.1026; **Fig. 2** ♂ RV; B.M.(N.H.) no. 1976.1027; **Fig. 3** ♂ RV; B.M.(N.H.) no. 1976.1028; **Fig. 4** ♂ RV; B.M.(N.H.) no. 1976.1029; **Fig. 5** juvenile −1 LV; B.M.(N.H.) no. 1976.1030; **Fig. 6** neotype, ♀ RV; B.M.(N.H.) no. 1976.1031. (All figures are stereo-pairs.)

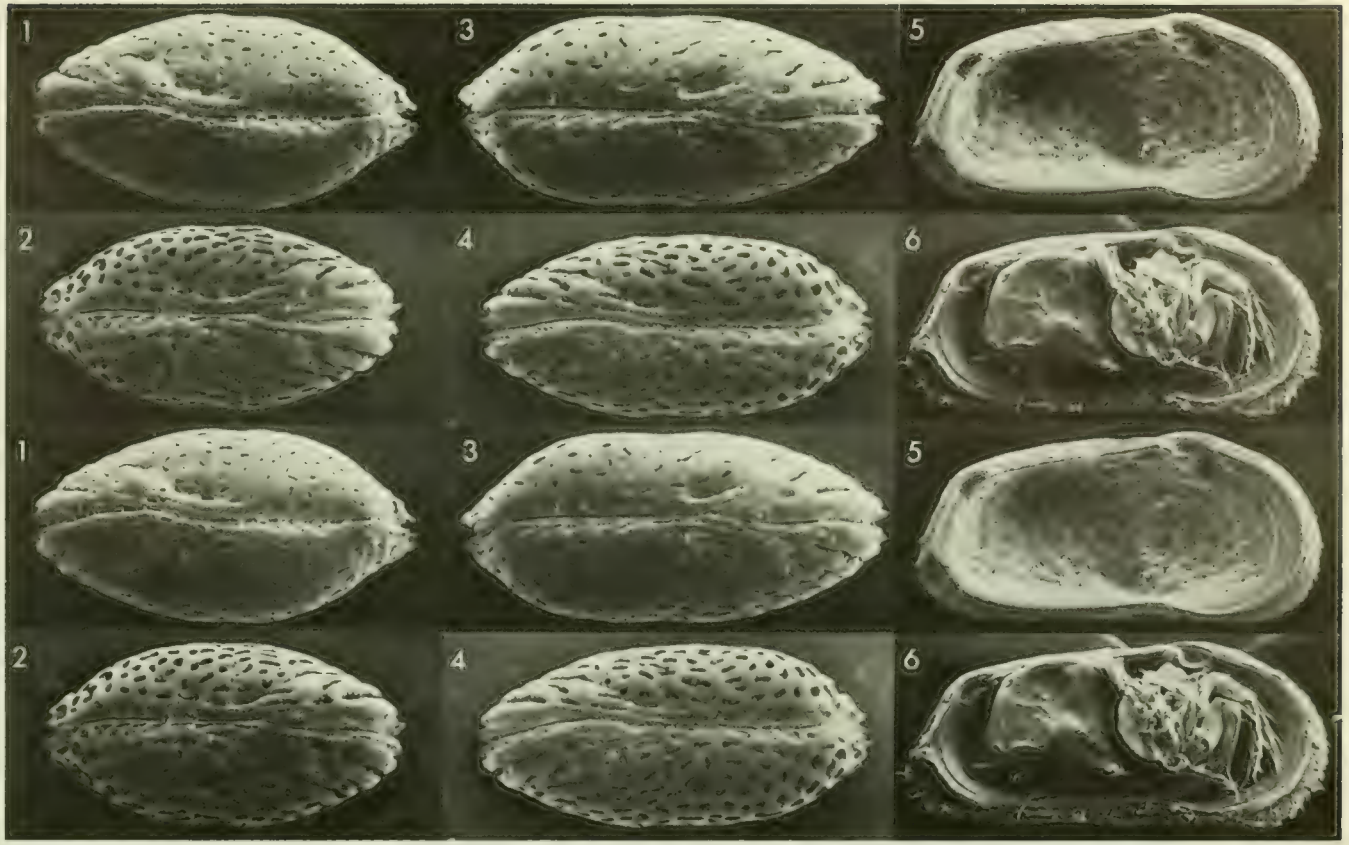


Plate 8 *Urocythereis distinguenda* (Neviani) (×60). **Fig. 1** ♀ dorsal carapace; B.M.(N.H.) no. 1976.1032; **Fig. 2** ♀ dorsal carapace; B.M.(N.H.) no. 1976.1033; **Fig. 3** ♂ dorsal carapace; B.M.(N.H.) no. 1976.1034; **Fig. 4** ♂ dorsal carapace; B.M.(N.H.) no. 1976.1035; **Fig. 5** ♂ LV; B.M.(N.H.) no. 1976.1036; **Fig. 6** ♂ LV and soft parts; B.M.(N.H.) no. 1976.1037. (All figures are stereo-pairs.)

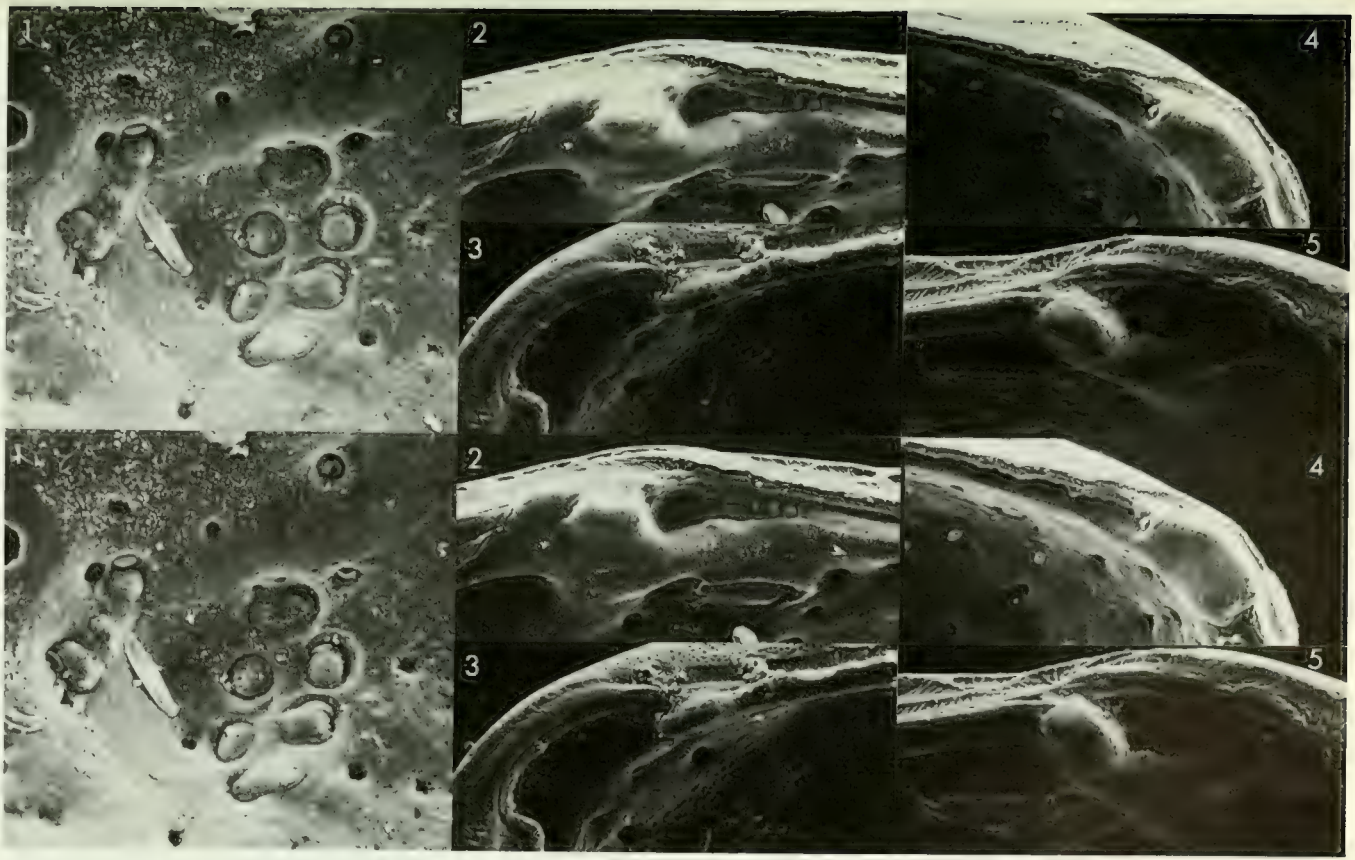


Plate 9 *Urocythereis distinguenda* (Neviani). **Fig. 1** ♂ RV, muscle scars; B.M.(N.H.) no. 1976.1038 (×290); **Figs 2, 4** ♂ RV, terminal hinge elements; B.M.(N.H.) no. 1976.1038 (×245); **Figs 3, 5** ♂ LV, terminal hinge elements; B.M.(N.H.) no. 1976.1040 (×245). (All figures are stereo-pairs.)

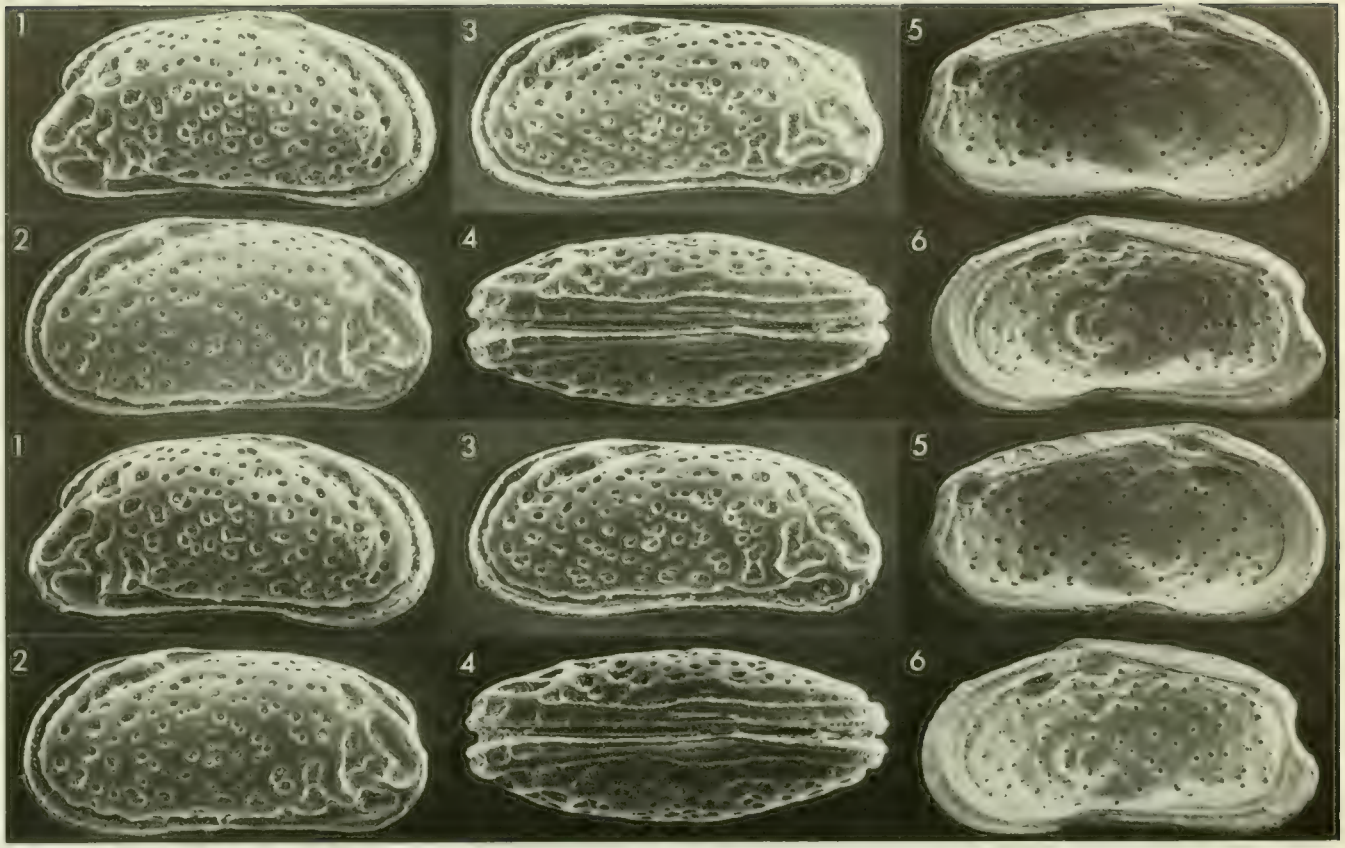


Plate 10 *Urocythereis flexicauda* Bonaduce, Ciampo & Masoli (× 76). **Fig. 1** ♀, RV; B.M.(N.H.) no. 1976.1054; **Fig. 2** ♀, RV; B.M.(N.H.) no. 1976.1055; **Fig. 3** ♀, LV; B.M.(N.H.) no. 1976.1056; **Fig. 4** ♂, ventral carapace; B.M.(N.H.) no. 1976.1057; **Fig. 5** ♀, LV; B.M.(N.H.) no. 1976.1055; **Fig. 6** ♀, RV; B.M.(N.H.) no. 1976.1058. (All figures are stereo-pairs.)

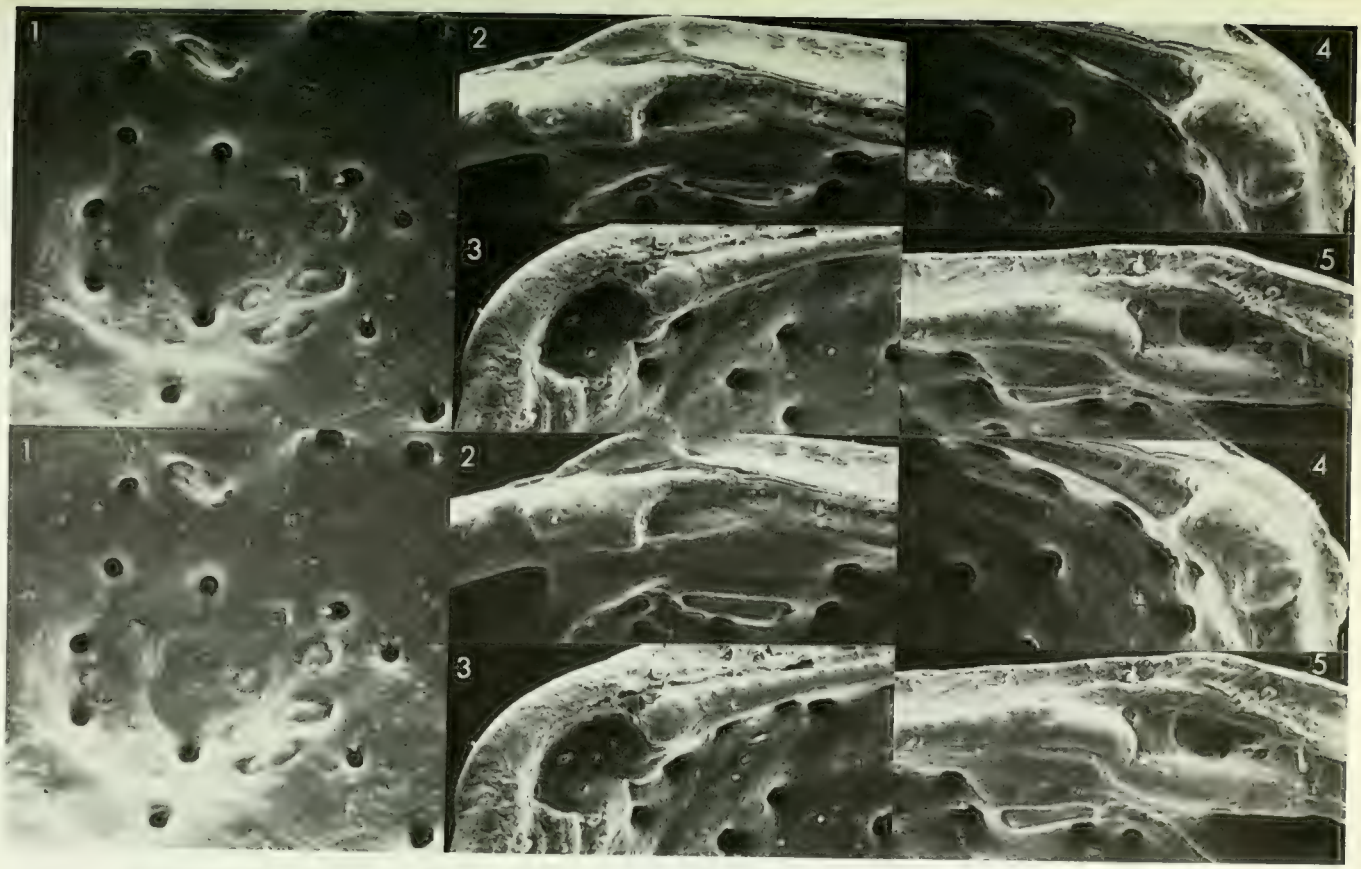


Plate 11 *Urocythereis flexicauda* Bonaduce, Ciampo & Masoli. **Fig. 1** ♀? RV muscle scars; B.M. (N.H.) no. 1976.1055 (×290); **Figs 2, 4** ♀? RV, terminal hinge elements; B.M.(N.H.) no. 1976. 1058 (×276); **Figs 3, 5** ♀? LV, terminal hinge elements; B.M.(N.H.) no. 1976.1055 (×276). (All figures are stereo-pairs.)

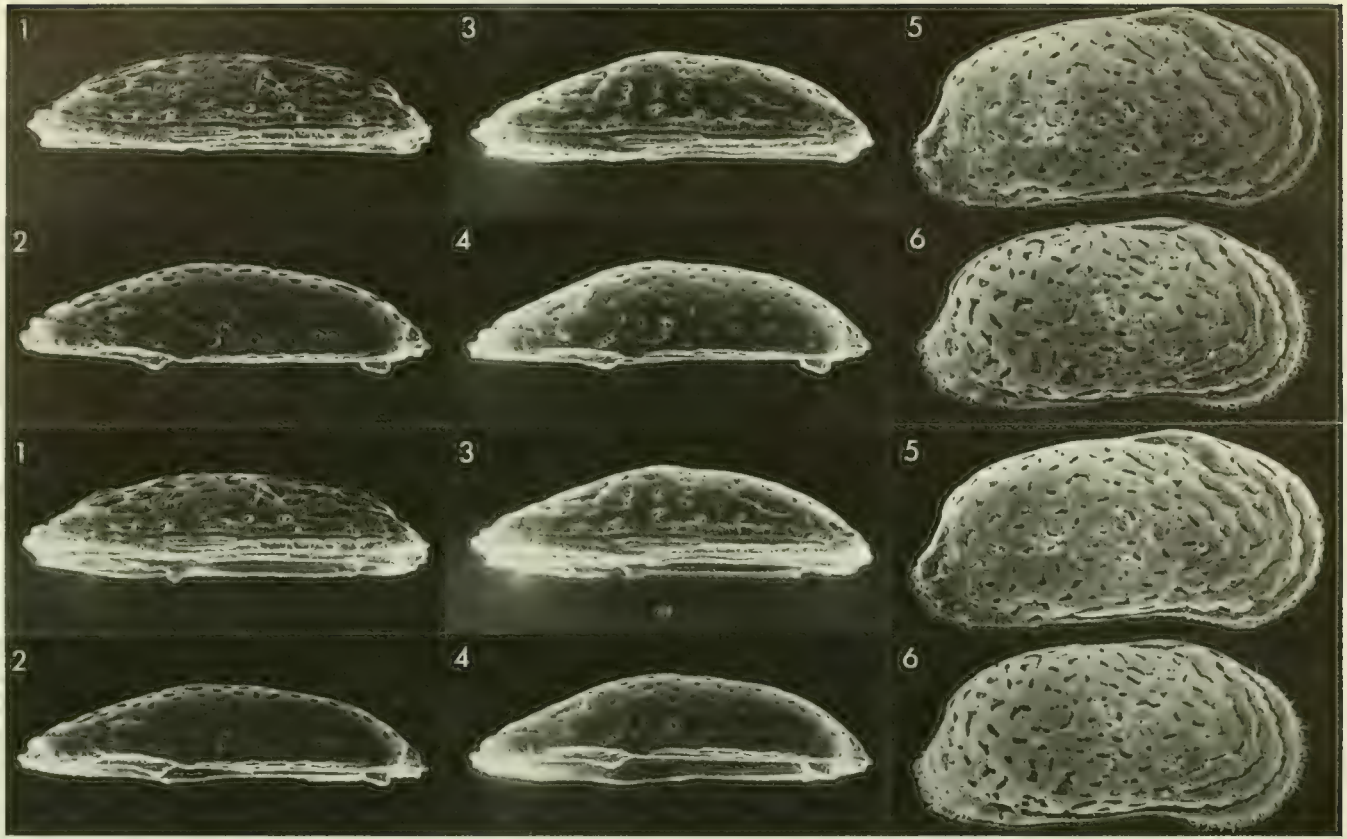


Plate 12 *Urocythereis margaritifera* (Müller) (×67). **Fig. 1** ♂ ventral LV; Müller collection no. 9296 (f); **Fig. 2** ♂ dorsal RV; Müller collection no. 9296 (f); **Fig. 3** ♀ ventral LV; Müller collection no. 9296 (g); **Fig. 4** ♀ dorsal RV; Müller collection no. 9296 (g).
Urocythereis distinguenda (Neviani) (×60). **Fig. 5** ♂ RV; B.M.(N.H.) no. 1976.1039; **Fig. 6** ♂ LV; B.M.(N.H.) no. 1976.1074. (All figures are stereo-pairs.)

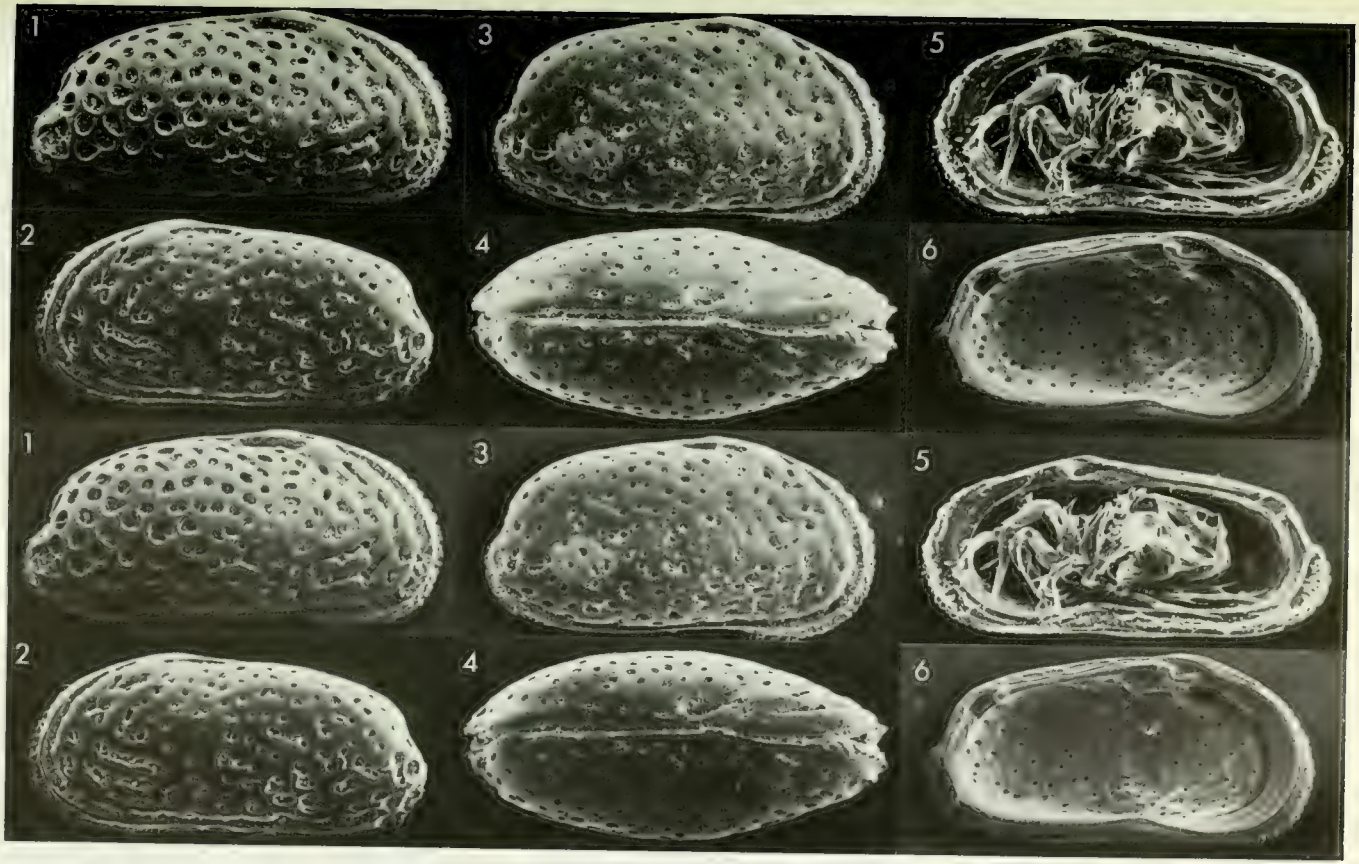


Plate 13 *Urocythereis margaritifera* (Müller) (× 67). **Fig. 1** ♂ RV; Müller collection no. 9296 (a); **Fig. 2** lectotype, ♂ LV; Müller collection no. 9296 (b); **Fig. 3** ♀ RV; Müller collection no. 9296 (c); **Fig. 4** ♂ dorsal carapace; Müller collection no. 9296 (d); **Fig. 5** lectotype, ♂ RV and soft parts; Müller collection no. 9296 (b); **Fig. 6** ♀ LV; Müller collection no. 9296 (e). (All figures are stereo-pairs.)

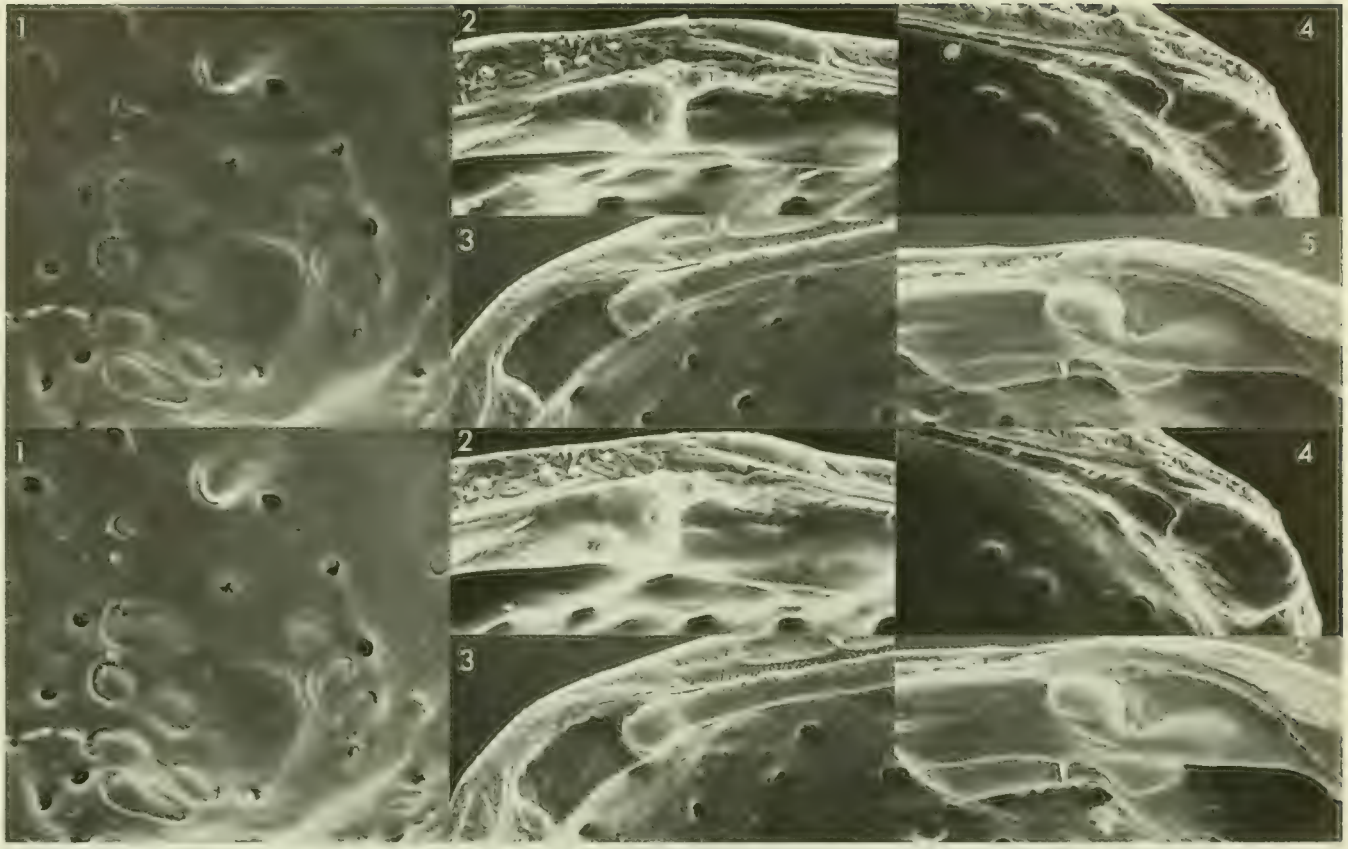


Plate 14 *Urocythereis margaritifera* (Müller). **Fig. 1** ♀ LV muscle scars; Müller collection no. 9296 (e) (× 255); **Figs 2, 4** ♂ RV, terminal hinge elements; Müller collection no. 9296 (f) (× 230); **Figs 3, 5** ♀ LV, terminal hinge elements; Müller collection no. 9296 (e) (× 230). (All figures are stereo-pairs.)

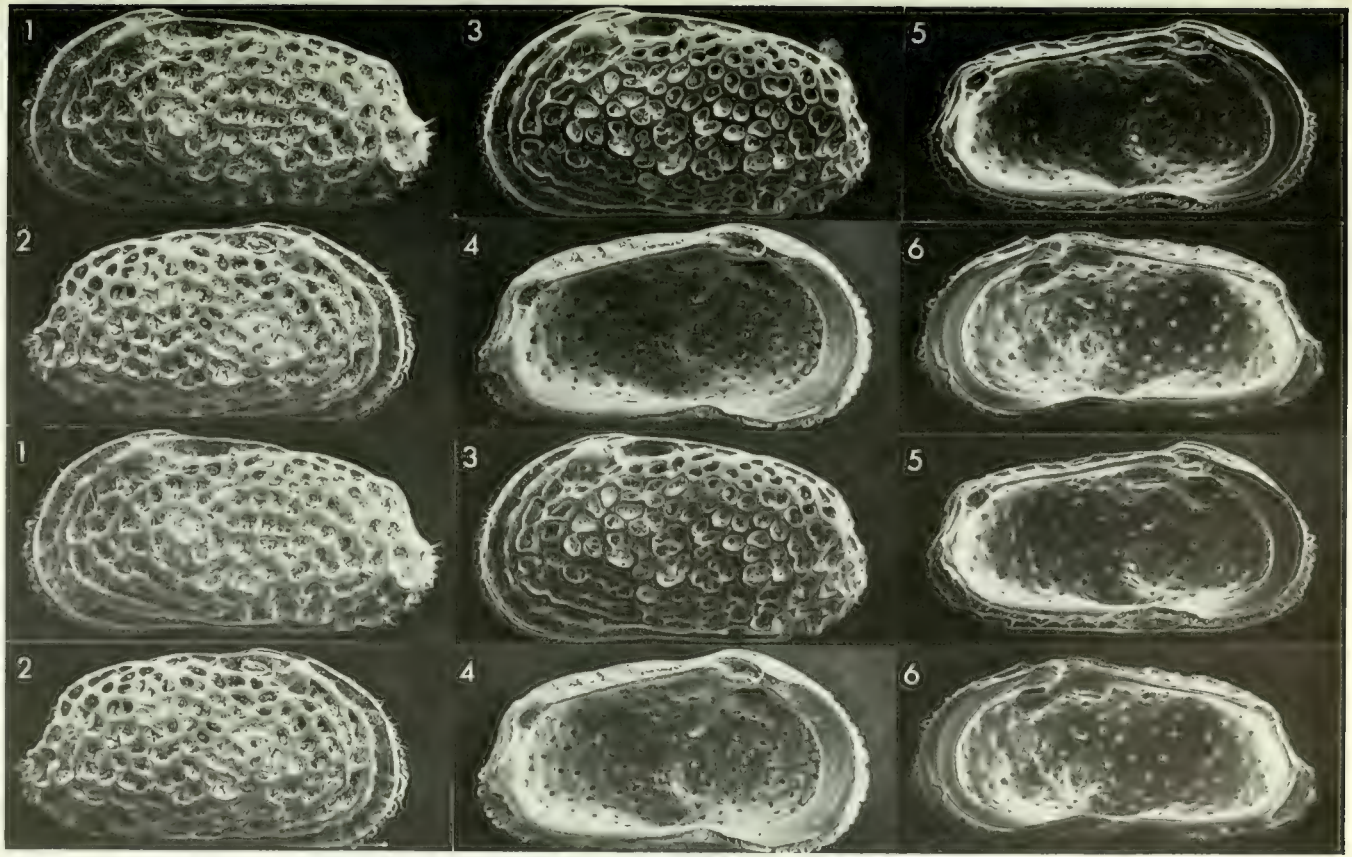


Plate 15 *Urocythereis neapolitana* sp. nov. (×60). **Fig. 1** ♂ LV; B.M.(N.H.) no. 1976.1059; **Fig. 2** ? ♀ RV; B.M.(N.H.) no. 1976.1060; **Fig. 3** ♀ LV; B.M.(N.H.) no. 1976.1061; **Fig. 4** ♀ LV; B.M.(N.H.) no. 1976.1062; **Fig. 5** holotype, ♂ LV; B.M.(N.H.) no. 1976.1063; **Fig. 6** holotype, ♂ RV; B.M.(N.H.) no. 1976.1063. (All figures are stereo-pairs.)

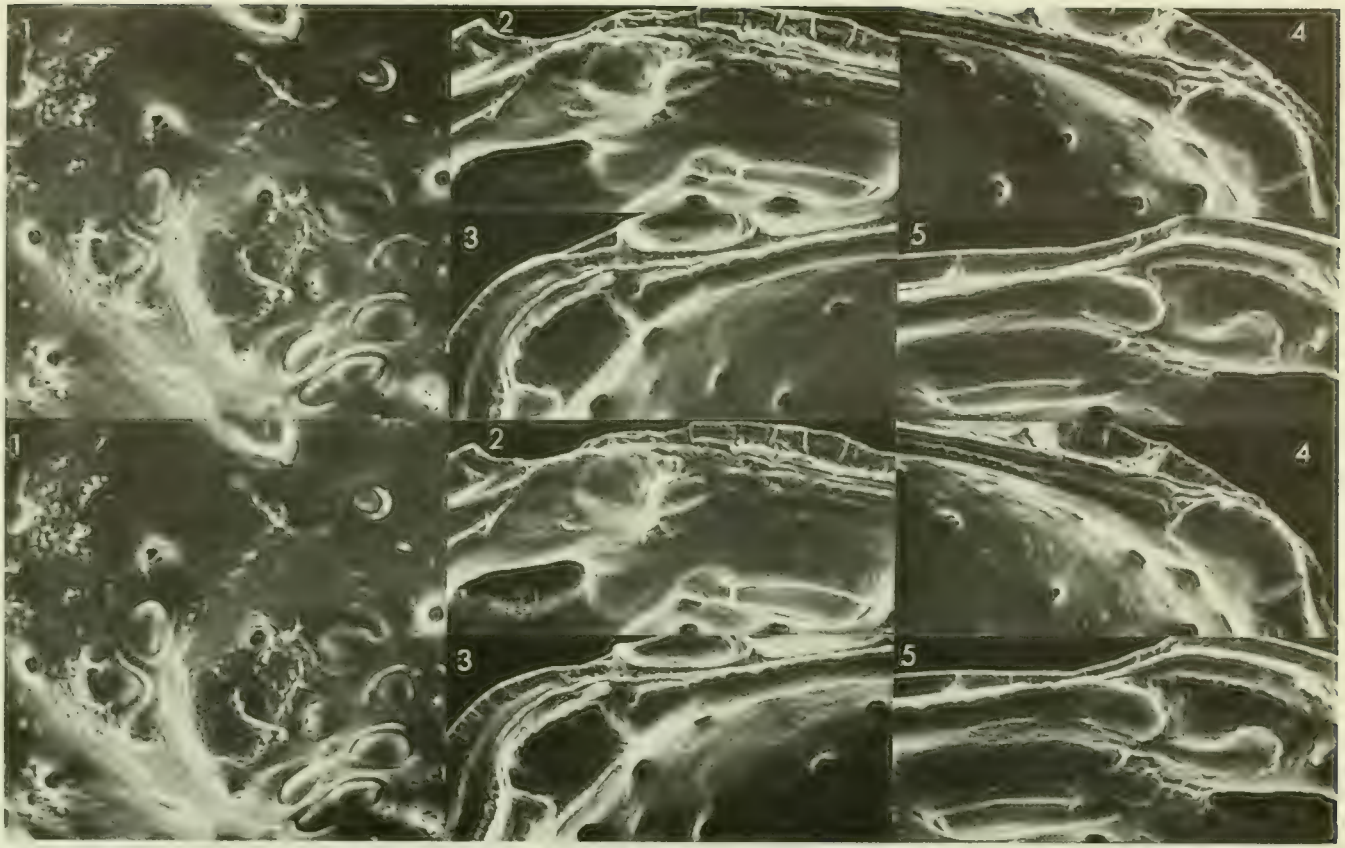


Plate 16 *Urocythereis neapolitana* sp. nov. **Fig. 1** ♀ RV, muscle scars; B.M.(N.H.) no. 1976.1063 (×290); **Figs 2, 4** holotype, ♂ RV, terminal hinge elements; B.M.(N.H.) no. 1976.1063 (×232); **Figs 3, 5** holotype, ♂ LV, terminal hinge elements; B.M.(N.H.) no. 1976.1063 (×232). (All figures are stereo-pairs.)

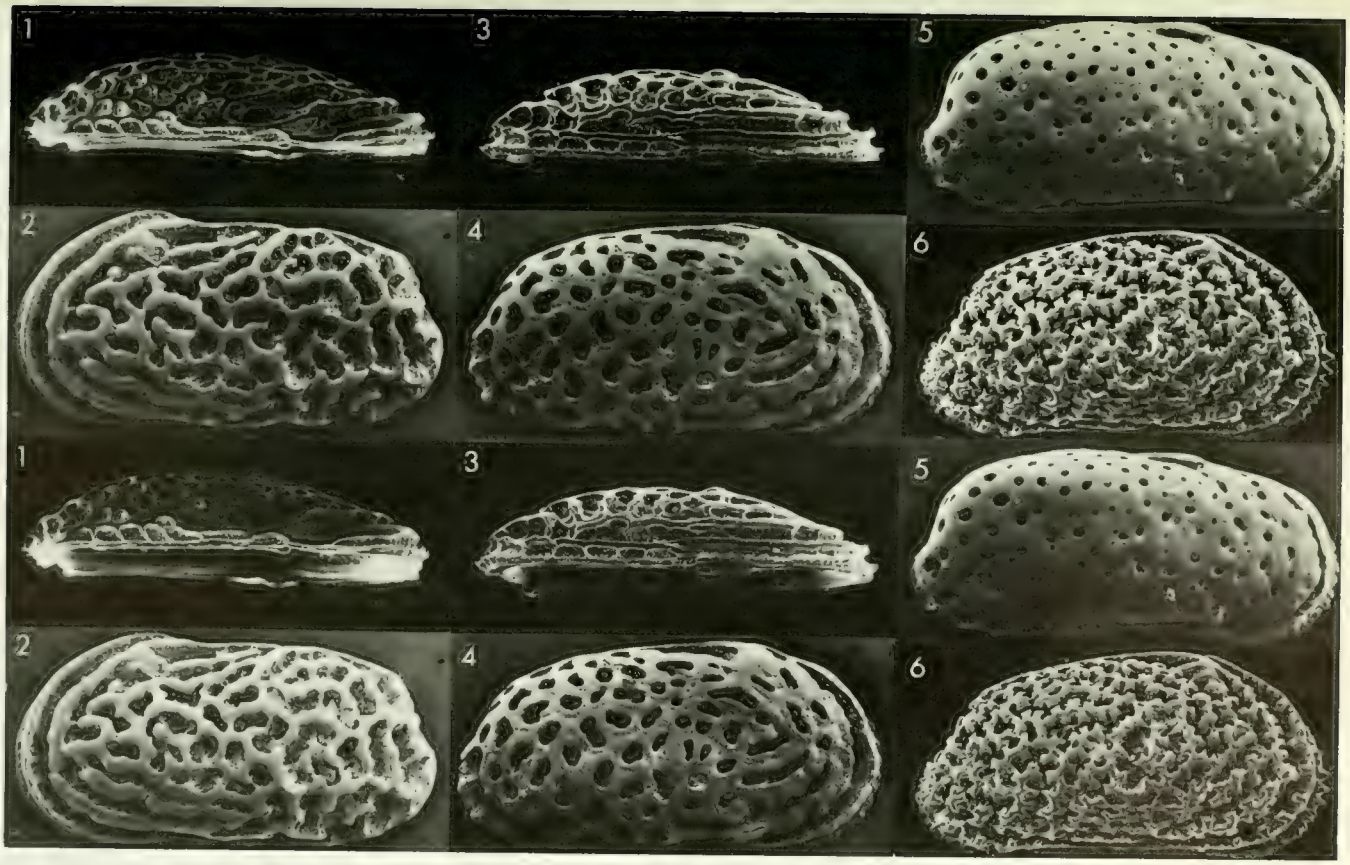


Plate 17 **Fig. 1** *Urocythereis neapolitana*; ♂ LV, dorsal; B.M.(N.H.) no. 1976.1064 (× 60); **Fig. 2** *Urocythereis* sp.; ? sex LV; B.M.(N.H.) no. 1976.1073 (× 59); **Fig. 3** *Urocythereis neapolitana*; ♂ RV, ventral; B.M.(N.H.) no. 1976.1065 (× 60); **Fig. 4** *Urocythereis* sp.; ? sex RV; B.M.(N.H.) no. 1976.1071 (× 59); **Fig. 5** *Urocythereis* sp.; ? sex RV; B.M.(N.H.) no. 1976.1072 (× 59); **Fig. 6** *Urocythereis phantastica* Athersuch & Ruggieri; ♀ LV; B.M.(N.H.) no. 1974.755 (× 63); Figs 2, 4 and 5 are from a single sample of beach sand from Tripoli, Libya. No specific assignment has been made as the material consists of only a few valves and carapaces without soft-parts. However, Figs 2 and 4 are probably variants of the same species. (All figures are stereo-pairs.)

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